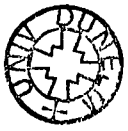
The relationship between the distribution of otter (*Lutra lutra*, L.) signs and habitat in the upper Tyne river catchment, NE England.

Timothy James Thom, B.Sc., M.Sc.

1997

Department of Biological Sciences

University of Durham



This thesis is submitted to the University of Durham for examination for the degree of PhD.

To

Gill (for everything)

THE RELATIONSHIP BETWEEN THE DISTRIBUTION OF OTTER (*LUTRA LUTRA*, L.) SIGNS AND HABITAT IN THE UPPER TYNE RIVER CATCHMENT, NE ENGLAND.

T. J. Thom

A Geographical Information System (GIS) and geostatistical methods were used to analyse patterns in the spatial distribution of otter signs in the upper Tyne river catchment. Spatial autocorrelation analysis showed that the distribution of otter signs in the catchment was geographically clumped. Otter signs were widespread in the spring and winter but restricted to the North Tyne and lower reaches of the South Tyne in the summer and autumn. The percentage occurrence of 1km, 600m and 200m stretches with otter signs present in the summer and autumn was significantly higher in the North Tyne than in the South Tyne.

Spraint analysis showed that salmonids (salmon and trout) formed the largest proportion of the fish prey in the diet in all seasons but minnows were as important as trout in the summer and autumn seasons. The occurrence of prey species in the diet broadly reflected the occurrence of those species in an electro-fishing survey in the summer of 1995. The majority of salmonids in the diet were in the >70≤90mm size class, significantly more than were in this class in the electro-fishing sample suggesting that otters actively selected this size of prey. Very small salmonids and minnows (<55mm) were also consumed in large numbers in the summer and autumn.

Logistic regression models were used to attempt to predict the distribution of otter signs in the upper Tyne catchment from environmental parameters at a variety of spatial scales. The majority of these logistic models failed. However, altitude was an important predictor in those models that did predict presence or absence of otter signs. It was argued that otters avoid high altitudes due to thermoregulatory constraints. Logistic regression showed that the presence of minnows was the best predictor of the differences in the percentage occurrence of otter signs between the North and South Tynes. It is tentatively suggested that heavy metal pollution is limiting minnow populations (and consequently the distribution of otters) in the upper Tyne catchment.

ACKNOWLEDGEMENTS

I would like to thank all the present and former members of the Tyne Otter Forum and their organisations - Dr. Chris Spray (Northumbrian Water); Dr. David Stewart, Lisa Kerslake, Andrew Bielinski (Northumberland Wildlife Trust); Dr. John Hoggar, Colin Blundell (National Rivers Authority); Steve Preston (Northumberland National Park) Bill Burlton (Forest Enterprise - Kielder District) and Pippa Merricks (English Nature) for funding and supporting this project.

I am indebted to Professor Peter Evans for his patience, support and advice during the period of the project. I am particularly grateful to him for ensuring that funding was available for the full three years of the study. I would also like to acknowledge the support and assistance of my other supervisors at Durham, Dr. Nigel Dunstone and Dr. Chris Thomas.

Mark Bailey and Dr. Mick Hanley deserve a special mention for enduring long hot days and Kielder midges during the electro-fishing surveys. Without their sterling efforts we would know a lot less about Tyne otters. Mark also assisted in the analysis of spraints for which I am indebted. I would also like to thank Tom Mercer for his work in analysing eel tissues and Dr. Martyn Lucas for his advice on electro-fishing methods.

I would like to extend my thanks to the other misfortunates in the lab who were also working on GIS projects - Larry Griffin, Sean Twiss, Mark O'Connnell and Phil Schwartz. The many discussions we had (both in the lab and the "other office"!) helped to shape some of the ideas in this thesis. I enjoyed my time working with such a diverse bunch of characters and wonder if such a group will ever be thrown together again.

I am indebted to all the landowners and angling clubs who allowed access to their properties and for letting me electro-fish their waters. Without their co-operation this kind of project could not go ahead.

I have reserved my biggest thanks to last for Gill Thom. In many respects she deserves this PhD more than me because of her kindness, patience and unwavering support over the last four years.

CONTENTS

1 GENERAL INTRODUCTION

This thesis describes the results of a detailed study of the distribution of otter signs in the River Tyne and its tributaries in north-east England and of the factors thought to influence these distributions. The study explored the use of a Geographical Information System (GIS) together with geostatistical methods to analyse geographical patterns in the distribution of otter signs at a variety of spatial scales. Multivariate statistical methods were used to determine whether the geographical distribution of environmental factors such as riverbank habitat type and prey availability could be used to predict the likelihood of specific stretches of river supporting otters.

The impetus for the study was a request from the Tyne Otter Forum (see Appendix I) for advice on management of the Tyne catchment to encourage an increase in the numbers of this "flagship" species for nature conservation in the region.

Strategies for the conservation of otter populations are dependent on a detailed understanding of their habitat requirements. There have been many studies which have attempted to determine what these habitat requirements are in environments ranging from exposed coastal areas to lowland rivers (for reviews see Chanin, 1985; Mason & Macdonald, 1986; Kruuk, 1995). However, many of these previous studies often fail to agree on otter habitat requirements even in similar environments. It is argued that there are a number of reasons for these differences of opinions. Many of the previous studies did not include all of those variables which may have been important in determining the distribution of otters. For example, many of the earlier studies focused on the availability of woodland vegetation along the riverbank which it was argued was related to the availability of suitable holt sites (e.g. Macdonald, Mason & Conghill, 1978; Macdonald & Mason, 1983; Bas, Jenkins & Rothery, 1984). However, none of these studies included detailed assessments of prey availability whereas in more recent studies it has been argued that this may be a major determinant of otter distribution (Kruuk, Carss, Conroy & Durbin, 1993).

In the majority of these previous studies a single sample unit size is used in the assessment of habitat selection by otters. In some studies the length of riverbank surveyed is large (e.g. 5km in Macdonald & Mason, 1983) while in others the sample

unit size is quite small (e.g. 50m in Bas *et al.*, 1984). These differences in sampling scale may lead to differences in the observed patterns in the distribution of otters which will depend on the kind of environmental parameters included in the analysis. For example, otters may view prey availability at a smaller scale (i.e. individual pools and riffles) than the availability of long stretches of secluded woodland for resting or breeding.

All of the past studies of otter distribution are descriptive in nature. That is, the number of otter signs or amount of time spent in a particular area is correlated with environmental variables and descriptive models of otter habitat utilisation produced. However, to my knowledge only one study has gone on to test the efficiency of these models in describing the distribution of otters in a particular area. Dubuc, Krohn & Owen (1990) developed a model predicting the occurrence of *Lutra canadensis* based on a number of habitat variables and tested the ability of the model to predict the presence of otter signs on a subset not involved in the original model construction.

No study of otter habitat requirements has taken account of the spatial distribution of otters or otter signs within the study area. Yet as Tobler (1970) stated in his "first law of geography"; "everything is related to everything else but near things are more related than distant things". When considering the distribution of objects in geographic space this will manifest itself as spatial autocorrelation (Cliff & Ord, 1973, 1981). The effects of this are discussed in more detail in chapter 3. but in general terms, positive autocorrelation can be considered as a result of attraction resulting in clumping. Negative autocorrelation on the other hand is the result of repulsion and results in the spacing-out of objects or organisms. Legendre (1993) argued that autocorrelation in both time and space was a very general property of all ecological systems. He argued that the environment is structured by large-scale physical processes (e.g. geomorphologic and meteorological processes) which cause the appearance of gradients or patchy structures separated by discontinuities. These large-scale processes induce similar responses in biological systems. Within these large-scale processes smaller scale biotic processes create more spatial structures through the processes of reproduction, mortality, predator-prey interactions, food availability and so on. Legendre (1993) thus argues that spatial patterns are not the result of random, noise-generating statistical processes but are an important phenomenon which is a function of ecosystem structure and becomes important in ecological studies. He argues that spatially distributed data

should be examined for spatial autocorrelation and, if it is found to be present, taken into account by modifying statistical methods. Liebhold, Rossi & Kemp (1993) describe a number of methods for doing this under the general heading of geostatistics and provide a number of examples of their use for entomological applications. Smith (1994) used logistic regression models which included additional variables to account for spatial autocorrelation in the distribution of mountain sorrel (*Oxyria digyna*) in the British Isles. A similar method was used by Augustin, Mugglestone & Buckland (1996) to model the spatial distribution of red deer (*Cervus elaphus*) in Scotland.

Chou, Minnich, Salazar, Power & Dezzani (1990) argued that, in the past quantification of spatial effects and incorporation of measures of spatial autocorrelation were technically prohibitive due to the difficulty in handling the large amounts of topological information associated with complicated ecosystems. This view was echoed by Liebhold *et al.* (1993) who argued that the complexity and difficulty of handling multi-dimensional data had hindered researchers in their attempts to understand spatial phenomena. However, they suggested that the development of GIS and geostatistical tools has now enabled spatial patterns to be examined in more detail.

Burrough (1988) defined a GIS as a set of computer programs that collect, store, retrieve, transform, display and analyse spatial data. Georeferenced data such as habitat type, otter spraint locations or fish densities can be incorporated into the GIS to produce map layers or coverages. A map layer is generally composed of only one type of data and therefore has a theme. The power of a GIS is that any number of themes that represent a particular area can be combined to form a full GIS database. The GIS then serves as a tool for analysing interactions among and within any combination of themes as long as they all have a compatible georeference. Geographical Information Systems are now widely used for ecological applications and there are a number of reviews which provide a detailed definition of GIS capabilities and applications (e.g. Burrough, 1988; Haines-Young, Green & Cousins 1993; Liebhold *et al.*, 1993). There is also software available such as SPACESTAT (Anselin, 1992, 1995) which can use data taken directly from the GIS to carry out geostatistical tests such as spatial autocorrelation analysis. Using these tools this thesis attempts to model the distribution of otters in the upper Tyne catchment in relation to habitat variables taking account of the spatial patterns in this distribution.

The thesis is set out in six main chapters including this introductory chapter. Chapter 2 provides a description of the study area. Chapter 3 describes spatial patterns in the distribution of otter signs in four different seasons in the upper Tyne catchment. There GIS and spatial autocorrelation analysis is used to describe the spatial structure of these distributions at a number of spatial scales. The mechanisms which cause spatial autocorrelation are also discussed. An important factor which may determine the distribution of otters is the availability of suitable prey. In chapter 4 spraint analysis methods were used to determine the composition of, and sizes of the main prey species in the diet of otters in the upper Tyne catchment. These data were compared with the results of an electro-fishing survey to determine whether otters were selecting particular sizes or species of prey. In chapter 5 multivariate statistical methods were used to attempt to predict the presence of otter signs from environmental variables. A wide variety of environmental parameters including riverbank vegetation type, holt availability, river width, depth and substrate type were recorded during the spraint surveys. In addition, the GIS was used to determine the altitude at each sample location. The GIS was also used to estimate the potential impact of human disturbance on otter distribution by measuring the lengths of roads and footpaths, area of buildings and presence of features such as car parks and picnic sites within buffers around the survey stretches. Prey availability data were collected during the electro-fishing survey outlined in chapter 4. In addition, an assessment of the level of heavy metal pollution in the catchment was made by analysing the concentrations of lead, zinc, cadmium and copper in the tissues of fifty eels caught during the electro-fishing surveys. Additional variables were also calculated which took account of the spatial autocorrelation in the distribution of otter signs as described in chapter 3. All of these variables were used to build logistic regression models which were used to attempt to predict the spatial distribution of otter signs in the upper Tyne catchment. Chapter 6 provides an overview of this study and discusses the importance of this research to the wider field of otter ecology and conservation. Future research needs are also discussed.

2 THE TYNE CATCHMENT

The Tyne catchment can be divided into three main river systems, the main Tyne, North Tyne and South Tyne. The North and South Tynes form the upland reaches of the catchment and this study focuses on these two rivers and associated tributaries (see Figure 2.1).

The North Tyne rises as a series of streams at an altitude of between 520-580m above sea level in the hills forming the border between England and Scotland. Within about 1km of its source it flows into the upper end of the Kielder Border forest, an extensive area of conifer plantation composed predominantly of Sitka and Norway spruce (*Picea sitchensis* and *Picea abies* respectively). Early plantings were established in the 1930s but it was not until the 1950s that the forest expanded and Kielder village was built. Within about 10km of the source the North Tyne's natural flow is interrupted by Kielder Reservoir which has a surface area of 1086ha and a maximum depth of 52m (Figure 2.1). Below Kielder Reservoir the North Tyne flows for a further 50km through predominantly rural areas, with sheep and cattle pasture comprising the main land-use. Kielder Reservoir now regulates the flow of water throughout much of the upper North Tyne.

Initially it was envisaged that the primary use of Kielder Reservoir would be to supply water to the region. This was achieved successfully and even in recent droughts elsewhere in the UK there have been few problems with water supply. However, in 1986 operating rules changed from an orientation to water supply to power generation (Johnson, 1988). Generators were installed in the dam which required a diurnal 16 hour cycle of releases at a rate of 15.4 cumecs which was ten times the compensation flow of 0.6-1.3 cumecs. In addition, maximum efficiency was obtained by drawing water from the bottom of the reservoir, which, due to thermal stratification, was at a different temperature to water in the river below the dam. The fish and invertebrate populations below the dam were studied by Haile, James & Sears (1989) and Haile (1992) who showed that invertebrate populations exhibited a marked reduction in both species diversity and abundance immediately below the dam. Further down the river, however, the invertebrate communities were much less affected and at 14km downstream of the dam they showed species richness and diversity comparable with other rivers in the

region. These studies also showed that salmon population densities were reduced in the area immediately below the reservoir and for the first 5km downstream although fish did spawn and hatch there successfully. This reduction in salmon densities was attributed to the silting up of hatched eggs by spring floods and a delay of several days between the swim-up period and the attainment of the 7^0C temperature required to initiate the onset of feeding in salmon fry. Further downstream many spawning sites were shown to be silting up with a steady decline in the numbers of underyearling salmon. It was also shown that releases of water from Kielder Reservoir had an effect on the temperature of the river but that this was restricted to a short stretch immediately below the dam.

However, in 1995, changes were made to the Kielder Reservoir water release pattern to provide a variable flow pattern similar to that expected to occur naturally based on the analysis of previous rainfall statistics. In addition to the compensation flow, releases for hydro-electric generation are now made on a three, five or seven day cycle, with the start day of each cycle varying and a choice of daily release times. In addition, the main generator produces power at two different flow rates of 14.1 and 9 cumecs. The water is also no longer drawn from the bottom levels of the reservoir thus reducing the effects of thermal stratification. It is envisaged that this variation in release rates and periods will have a beneficial effect on the ecology of the North Tyne.

There are a number of small tributaries and streams which flow into the reservoir and the North Tyne but only one of these is significant enough to be classed as a river. The River Rede is an upland river of 43km in length and is at the north eastern extremity of the North Tyne system. Its source is at an altitude of about 408m above sea level and, like the North Tyne the river's natural flow is altered after about 7km by the presence of Catcleugh Reservoir (Figure 2.1). The human population of Redesdale is low and the river flows through few urban or industrial areas with much of the Rede catchment taken up by the Ministry of Defence Otterburn Training Area. The upper part of the river flows through Kielder Forest and the remainder of the catchment is composed predominantly of mainly sheep and cattle pasture.

The South Tyne rises at an altitude of about 500m in the hills forming the boundary between the counties of Cumbria, Durham and Northumberland. It has two main tributaries, the River Nent and the River Allen, and its flow is unrestricted by the

reservoirs and afforestation so characteristic of the North Tyne catchment. Although mainly rural, the river does flow through one industrial area in Haltwhistle but the predominant feature of the South Tyne is the history of mineral extraction from the North Pennines orefield in its headwaters. The majority of mining activity has now ceased but the legacy still remains in the form of mine drainage water. The River Nent still contains high levels of zinc and lead (Say & Whitton, 1981) and work by Abel & Green (1981) demonstrated high levels of heavy metal pollution in the rivers East and West Allen. These extend for about 18km and drain adjacent valleys which were extensively mined in the 18th and 19th centuries. Zinc bearing veins were confined to the West Allen and waste heaps still remain. In the East Allen valley much of the mining was for lead and waste heaps were removed whilst work was in progress. Abel & Green (1981) showed that the West Allen contained 10 times higher levels of zinc than the East Allen and that cadmium was also present. In addition to chemical differences, invertebrate populations were also restricted in the West Allen and thus may have had a significant impact on fish populations. These polluted tributaries flow into the South Tyne and may have had a significant impact on the ecology of the river as a whole.

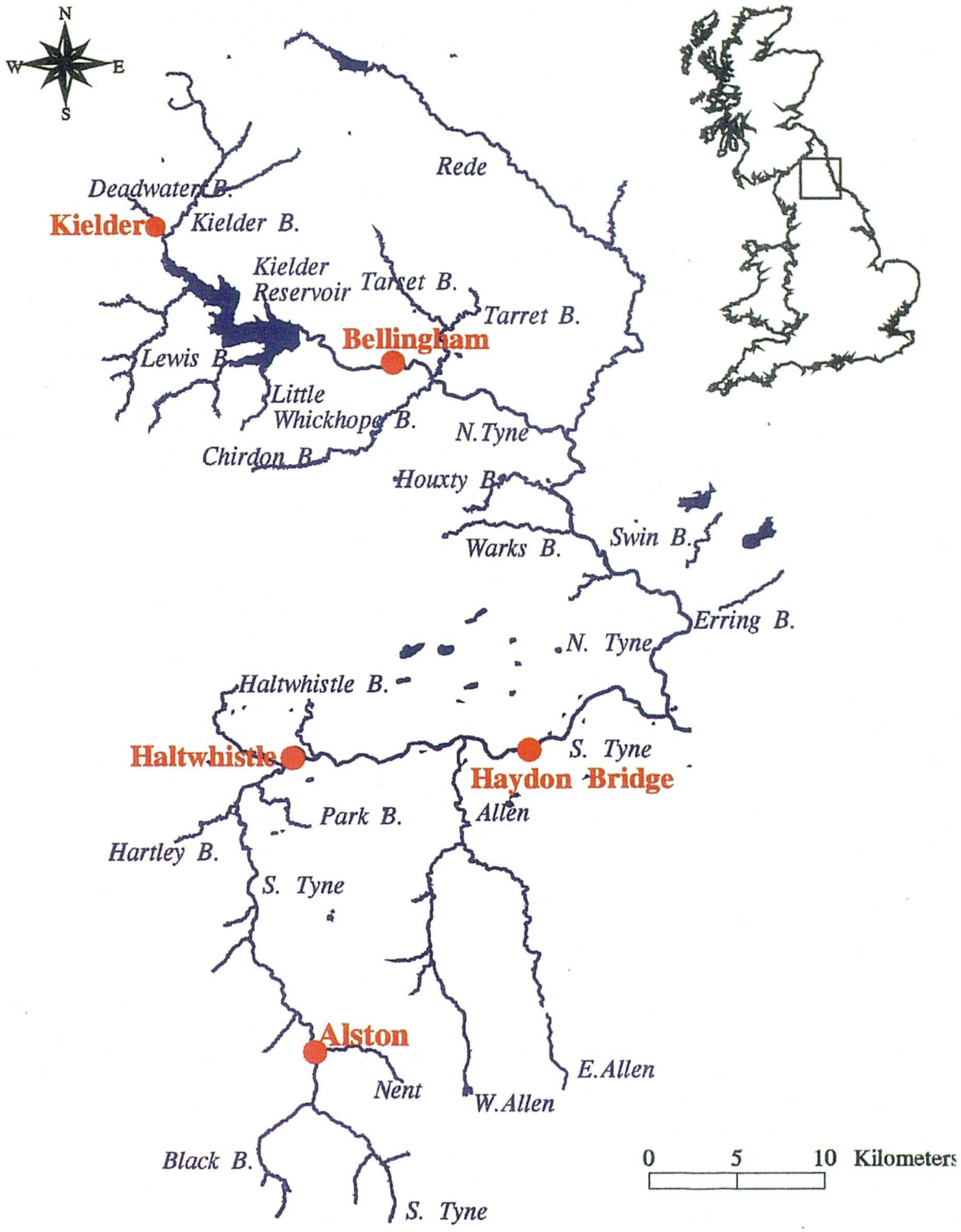


Figure 2.1 The Tyne catchment showing the North and South Tyne study area.

3 THE SPATIAL DISTRIBUTION OF OTTER SIGNS IN THE UPPER TYNE CATCHMENT

3.1 INTRODUCTION

This chapter describes the pattern of distribution of otter signs in the upper Tyne catchment. The effect of changes in spatial sampling scales are considered and seasonal and geographical differences in the distribution of otter signs are explored.

3.1.1 Describing spatial patterns in distributions.

Jenkins & Burrows (1980) showed that the frequency distribution of the number of otter signs in 2km stretches of riverbank on the river Dee, Aberdeenshire was clumped by comparing it with a theoretical random (Poisson) distribution. Bas *et al.*, (1984) also demonstrated clumping in the distribution of otters in Deeside using indices of dispersion. Trowbridge (1983) used nearest neighbour analysis to show that, for coastal otters spraints were clumped into 'stations' but these were evenly spaced along the coastline at 40m intervals. There are, however, major limitations of these methods for detection of pattern in distributions as described in Appendix II. The first is that they do not utilise all the information available on the pattern of the distribution. Quadrat based methods, and indeed the majority of standard statistical techniques, look only at the frequency distribution of the attributes without making any reference to the spatial location of the sampling units. Order-neighbour methods deal with spatial location to a limited extent but make no reference to the attributes of the sampling units and are limited to a maximum of third order neighbours. Second, the majority of the statistical tests outlined in Appendix II are based on the fact that individual sampling locations are independent of one another. However, when considering the pattern of spatially distributed data, geographical proximity of sampling locations may mean that this is not the case. This is due to the phenomenon of spatial autocorrelation where sampling units which are close in geographic space are more likely to be similar in their attributes and therefore not independent of each other. In fact, as Gould (1970) states;

"All our efforts to understand spatial pattern, structure and process have indicated that it is precisely the lack of independence - the interdependence - of spatial phenomena that allows us to substitute pattern and, therefore, predictability and order for chaos and apparent lack of interdependence of things in time and space".

Spatial autocorrelation analysis overcomes both of these problems since it deals simultaneously with both locational and attribute information and tests for the interdependence of spatially distributed objects (Cliff & Ord, 1973, 1981; Sokal & Oden, 1978a, 1978b; Goodchild, 1986; Haining, 1990) Spatial autocorrelation analysis therefore provides a much better estimate of spatial patterns in the distribution of otter signs. In this method a pair of spatial sampling units may be similar or dissimilar in attributes, such as habitat type or river width and their geographical proximity will determine how similar they are in spatial location. In its broadest sense spatial autocorrelation compares these two sets of similarities. If features which are similar in location also tend to be similar in attributes, then the pattern shows positive spatial autocorrelation. Conversely, negative spatial autocorrelation exists when features which are close together in space tend to be more dissimilar than features which are further apart. Finally, the case of zero spatial autocorrelation occurs when attributes are independent of location. As an index, spatial autocorrelation analysis provides information about a spatially distributed phenomenon which is not available in any other form of statistical analysis. If a spatial distribution of unequal attributes was to be summarised into a single statistic, a spatial autocorrelation index would be chosen just as we would choose a measure of central tendency such as a mean or median to summarise a non-spatial distribution.

Southwood (1977) argued that when a population was sampled three basic bits of information were available, mean, variance and sample size. For a spatially distributed population we now add a fourth piece of information - a measure of spatial autocorrelation.

3.1.2. Effect of sampling scale

All of the statistical methods outlined in Appendix II are influenced by differences in sampling scale yet, as Wiens (1989) argued, many ecologists behave as if the patterns

and the processes that produce them are independent of differences in spatial scale and in many studies the effect of changes in scale has been ignored. However, Wiens (1989) provided a number of examples which demonstrated that the scale of an investigation may have profound effects on the patterns found. For example, in the Great Barrier Reef the distribution of fish species among coral heads on a single atoll or reef may be influenced by unpredictable chance events making species composition unpredictable. At the broader scale of whole reef systems community composition is more predictable. The distribution of phytoplankton in marine systems is dominated by horizontal turbulent diffusion at scales of about 1km. At broader scales, phytoplankton growth, zooplankton grazing and vertical mixing override these effects. O'Neill, DeAngelis, Waide and Allen (1986) argued that the detection of pattern is determined by both the 'extent' and 'grain' of an investigation where extent is the overall area encompassed by a study and grain is the size of the individual units of observation. Extent and grain define the upper and lower limits of resolution of a study and for logistical reasons, expanding the extent usually entails enlarging the grain. The enhanced ability to detect broad-scale patterns carries the cost of a loss of resolution of fine-scale details. Table 3.1.1 shows how the characteristics of ecological systems at fine scales differ from those at broad scales. The scale of investigation thus determines the range of patterns and processes that can be detected. It is essential, therefore, that we study a system at an appropriate scale otherwise we may fail to detect its actual dynamics and patterns but may instead find patterns that are artefacts of scale.

3.1.3 Objectives of this chapter

The work outlined in this chapter has three main objectives in considering the pattern of distribution of otter signs in the upper Tyne catchment;

(i) to describe spatial patterns in the distribution of otter signs,

(ii) to investigate the effects of changes in scale (grain) on the patterns described above,

(iii) to investigate seasonal differences in the distribution of otter signs in the upper Tyne catchment.

Table 3.1.1 Characteristics of various attributes of ecological systems and their investigation at fine and broad scales of study. Adapted from Wiens (1989).

Attribute	Scale	
	Fine	Broad
Number of variables important in correlations	Many	Few
Type of heterogeneity	Patch	Landscape mosaic
Factors influencing species' distribution	resource distribution, physiological tolerances	barriers, dispersal
Resolution of detail	High	Low
Sampling adequacy (intensity)	Good	Poor
Effects of sampling error	Large	Small
Replication	Possible	Difficult
Empirical rigour	High	Low
Potential for deriving generalisations	Low	High
Form of models	Mechanistic	Correlative
Testability of hypotheses	High	Low
Surveys	Quantitative	Qualitative

3.2 METHODS

3.2.1 Field surveys

Forty 5km survey stretches of riverbank were measured from 1:10000 scale Ordnance Survey Maps using a map measurer initially but later more accurately measured from digitised maps in the GIS. Figure 3.2.1 shows the locations of the 5km stretches. Five kilometres was chosen as a survey distance for two main reasons;

(i) this distance could be surveyed in one day, hence each survey was completed in less than two months (taking into account bad weather conditions) thus allowing repeat surveys at different seasons;

(ii) this was considered to be a distance that could be surveyed without loss of effort due to fatigue or failing daylight in the winter months.

Along each 5km stretch a 10m width of one bank and any rocks or logs in the water up to the middle of the watercourse were searched for signs of otters. The bank to be searched was randomly chosen prior to the survey. All surveys were conducted during periods of low water and at least four days after any periods of heavy rain or water releases from Kielder Reservoir. The locations of all signs found were recorded on 1:10000 scale Ordnance Survey maps.

Spraints were searched for on rocks, large tree root systems, overhanging branches, holes in the bank and other sites along the riverbank. Where likely spraint sites were inaccessible, for example on rocks in deep water, binoculars were used to look for otter signs.

Tarry secretions (believed to be the same material that binds spraints together) and mucus-like deposits varying from white to brown in colour and with the characteristic otter smell were also recorded. Paths, flattened areas and above ground resting sites were also recorded if these could be attributed to otters. This usually depended on the presence of other signs such as spraints along paths or spread around flattened areas.

Spraint heaps (areas of sand or mud scraped into a mound, often with a spraint on top) were also recorded.

Each survey was carried out four times so that the effects of seasonal changes on the distribution and abundance of otter signs could be assessed. The survey periods were Spring 1993 (1st of March to 30th of April), Summer 1993 (10th of June to 10th of August), Winter 1994 (January 5th to February 28th) and Autumn 1994 (October 1st to November 20th). The Autumn survey was conducted in 1994 because a serious road accident prevented the completion of this survey in 1993.

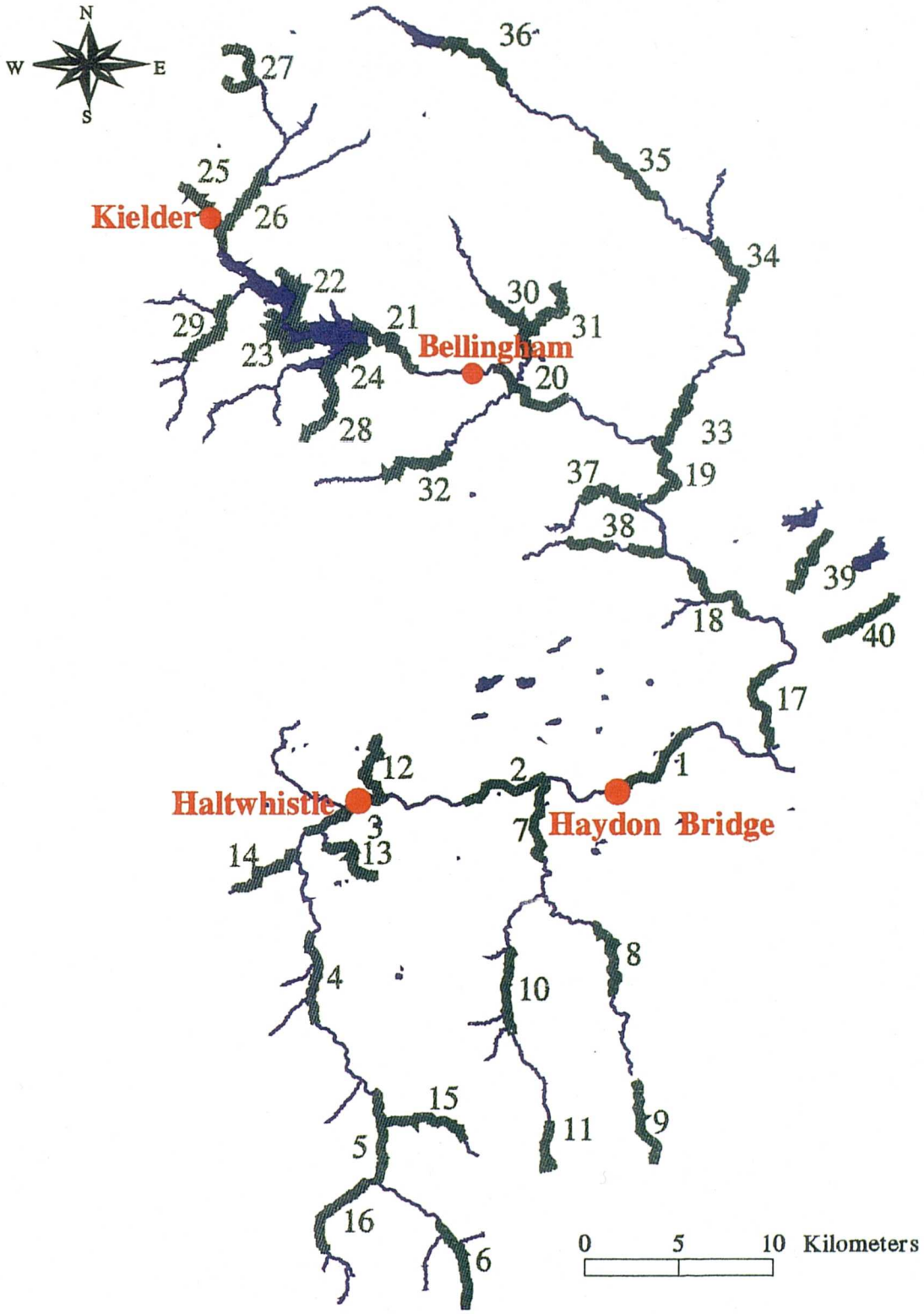


Figure 3.2.1: Map of the upper Tyne catchment showing forty 5km stretches (bold lines) of riverbank surveyed for otter signs during four seasonal surveys between March 1993 and November 1994.

3.2.2 Data handling

Creating a GIS basemap

Arc/Info version 6.0 and later version 7.0 running under UNIX on a Sparc workstation was used to create a GIS basemap of the Tyne catchment area. Small streams, rivers and lakes, reservoirs and ponds were digitised from 1:25000 scale Ordnance Survey maps. These were stored as three separate data layers (coverages) - *STREAM, RIVER* and *LAKE* respectively. In addition, separate line coverages of major and minor roads (*AROADS* and *BROADS* respectively), footpaths and bridleways (*PATHS*) and a polygon coverage of buildings (*BUILDS*) were also digitised. Point coverages of camping and picnic sites were also created. A map of 50m contours was obtained from Bartholomew's maps (available to the University in digital form) and used to create a digital terrain model using the Arc/Info TIN routines. This was then used to determine altitude at selected locations in the catchment (see chapter 5).

Transferring spraint locations to the GIS

The *RIVER, STREAM* and *LAKE* coverages described above were converted into a single line coverage called *SPATNET.* A number of arcs in this new coverage which corresponded to each 5km stretch were selected in Arcedit. These were then converted into a Dynamic Segmentation (see Appendix III) route system using the MAKEROUTE command.

The results of the spraint surveys were input into the GIS in two ways. First, the location of each sign was digitised into a point coverage from the 1:10000 scale maps used in the field. The x,y co-ordinates of each sign were then converted to point events in a Dynamic Segmentation event table using the ADDROUTEMEASURE command to link them to the correct 5km stretch in the route system created above. Second, the halfway point was used as the centroid for each 5km stretch and was stored as a Dynamic Segmentation point event table (*SPACORR.5KM*). This table also contained variables giving the total number of spraints and spraint sites for each 5km stretch in each seasonal survey and binary variables of presence or absence of otter signs in each 5km stretch in each season. These centroids were used to create a point coverage using the

Dynamic Segmentation command EVENTPOINT and this coverage was then converted to an ASCII file of x,y co-ordinates using the Arc command UNGENERATE. This file was used in an Arc/Info programme to create new nodes in the *SPATNET* coverage corresponding to the centroid of each 5km stretch and to save the label-ids of these nodes back into the *SPACORR.5KM* event table for subsequent use in Network Analysis (see Appendix III).

Spatial analysis of spraint distribution patterns.

The analysis of spatial autocorrelation required two sets of information. First, a data file containing attributes, in this case the number of spraints and spraint sites and the presence or absence of otter signs in each 5km stretch. This information was stored in the *SPACORR.5KM* event table. Second, a spatial weights matrix which describes the spatial distribution of sampling locations. This is conveniently provided by a matrix of distances between each sampling location and all of its neighbours usually calculated as Euclidean distances between x,y co-ordinates. However, in this study otter signs were restricted to a narrow strip of riverbank and indeed it is well-established that otters mostly utilise habitats close to watercourses (Kruuk, 1995). Therefore, intuitively it would be more appropriate to calculate distances along the routes that otters were likely to follow, that is along the riverbank, and not Euclidean distances. Without a GIS this would be almost impossible to do with accuracy. However, Arc/Info Network Analysis provides a suite of tools for the analysis of the distribution of locations along linear networks (see Appendix III). Network Analysis requires that sampling locations are recorded as nodes in a coverage containing arcs (the network coverage) and that attribute data are stored in a separate file which relates to these nodes and is called the centres file. For this study these files were provided with the creation of *SPATNET* (the network coverage) and *SPACORR.5KM* (the centres file). The Network Analysis command NODEDISTANCE was then used to create a matrix of the network distances (non-Euclidean) between 5km centroids using these two files. Once the matrix and data files were produced spatial analysis was carried out using a software package called SPACESTAT (Anselin, 1992 & 1995). With a few minor modifications the distance matrix created in Network Analysis and the variables contained in *SPACORR.5KM* were converted to ASCII files for subsequent use in SPACESTAT (see below).

The existence and type of spatial autocorrelation in a dataset will be determined by how far apart the sampling locations are in geographic space. For example, positive autocorrelation may be present if two neighbouring stretches are close together but as the distance between stretches increases autocorrelation may not be evident or may even become negative. Therefore, more information about the spatial pattern of the distribution can be obtained if autocorrelation is assessed at a series of distances between sampling locations. This was achieved in SPACESTAT by converting the distance matrix into a series of binary contiguity spatial weights matrices using a series of distance filters. For example, the level of spatial autocorrelation between 5km stretches that are 10km apart can be determined by using a filter to produce a spatial weights matrix where 5km stretches which are contiguous (neighbours) at this distance are given a 1 and all others are given a zero and then using this matrix in the spatial analysis. This process is repeated using a number of desired distance filters. Table 3.2.1 gives the distance filters used in the analysis of spatial autocorrelation between 5km stretches in this study.

Table 3.2.1 Distance filters used to create binary contiguity spatial weights matrices used in the analysis of spatial autocorrelation in the distribution of otter signs between 5km, 2.5km, 1km, 600m and 200m stretches of riverbank in the upper Tyne catchment.

Filter	Distance				
	5km scale	2.5km scale	1km scale	600m scale	200m scale
1	>5≤10km	≥2.3≤2.7km	≥0.8≤1.2km	≥1.1≤1.3km	≥150≤250m
2	>10≤20km	≥5<10km	≥2.8≤3.2km	≥2.3≤2.5km	≥1.95≤2.05km
3	>20≤30km	≥10<20km	≥5<10km	≥3.5≤3.7km	≥3.95≤4.05km
4	>30≤40km	≥20<30km	≥10<20km	≥5<10km	≥5<10km
5	>40≤50km	≥30<40km	≥20<30km	≥10<20km	≥10<20km
6	>50≤75km	≥40<50km	≥30<40km	≥20<30km	≥20<30km
7	>75≤100km	≥50<75km	≥40<50km	≥30<40km	≥30<40km
8	-	≥75≤100km	≥50<75km	≥40<50km	≥40<50km

Two types of analysis were used to determine the level of spatial autocorrelation in the distribution of otter signs in 5km stretches of riverbank in the upper Tyne catchment depending on the type of attribute variable used. Moran's I (Moran, 1948) (see Appendix IV) was used to determine the level of spatial autocorrelation between 5km stretches in each season using the total number of spraints or spraint sites per 5km stretch as the attribute. Alternatively, when the presence or absence of otter signs was used as the attribute variable, the method of Join counts (see Appendix IV) was used as a measure of autocorrelation at each distance in each season.

Spatial analysis using smaller sample unit sizes.

As discussed in the introduction to this chapter distribution patterns are affected by the extent (size of the study area) and grain (size of sampling units) of the investigation. The overall aim of this study was to investigate the distribution of otter signs over a whole catchment and there was little merit, therefore, in investigating the effect of changes in extent. There was, however, merit in investigating the effects of changes in the grain of the study since these may have profound effects on the detection of patterns in the distribution of otter signs in the Tyne catchment. Therefore, the 5km stretches were sub-divided into smaller sampling units using Dynamic Segmentation tools. In a preliminary analysis of these data (Thom, Thomas, Dunstone & Evans, in press) 50m was used as the smallest sample unit but it was shown that the results obtained using this sample unit size were no different to those obtained using a 200m sample unit size therefore this was used as the smallest sample unit size in this thesis. Other sample unit sizes were chosen to reflect the most common sampling scales used in recent literature, that is 1km (Delibes, Macdonald & Mason, 1991) and 600m (e.g. Strachan *et al.*, 1990). In addition, a sample unit size of 2.5km was used which was approximately half way between the 600m/1km and 5km sample unit sizes. Centroids for each sample unit at each of these scales were calculated as for the 5km sample units and converted into a data file and distance matrix using the same methods as before. Measurement errors of between 50-100m in the mapped length of the 5km sample units which were too small to drastically affect the results at this scale became more influential at smaller unit sizes. Therefore, each 5km stretch was not always fully divided into the smaller sample units. Two of the 5km stretches (11 and 27) consisted of a number of non-continuous upland streams giving a total length of 5km and it was difficult to sub-divide these into smaller unit sizes.

Therefore, these two stretches were not used in the analysis of the effects of changing the sample unit size. At the 200m unit size the resultant distance matrix was too large to be manageable (944 sample locations); therefore it was reduced in size by using only those 200m stretches which produced otter signs in any season (248 stretches) and a random selection of 250 stretches which produced no otter signs in all seasons. Although this resulted in a loss of information, the sample size was still large enough to detect significant patterns in the spatial distribution of otter signs. All spatial autocorrelation analyses were carried out in SPACESTAT as for 5km stretches. Additional distance filters were used to detect patterns of spatial association at short distances between sample units and these are given in Table 3.2.1. All non-spatial statistical analysis was carried out using Microsoft Excel spreadsheets and SPSS for Windows (Norusis, 1993a, 1993b, 1993c).

3.3 RESULTS

3.3.1 SIGN versus SITE.

The number of tarry secretions, mucus-like deposits and other scent marks was so low for all surveys that these were combined with the number of spraints per 5km stretch into one category called SIGN. A second category, SITE, was also established as the number of scent marking sites per 5km stretch. Each SITE was defined as a location containing one or more SIGN separated by at least 1m from another location containing one or more SIGN. Appendix V gives the total number of SIGN and SITE found along each 5km stretch of riverbank in each season. Summary statistics for the number of SIGN and SITE in 5km stretches are provided in Table 3.3.1. Table 3.3.2 gives the results of Wilcoxon Signed-Ranks Tests (T statistic) of differences between the number of SIGN and the number of SITE per 5km stretch in each season. In all cases the number of SIGN per 5km stretch differed significantly from the number of SITE. Kruskal-Wallis One-Way ANOVA (H statistic) tests showed that the median number of SIGN and SITE per 5km stretch did not differ significantly between seasons (SIGN; $H_3 = 5.8$, NS; SITE, $H_3 = 5.6$, NS, both corrected for ties). However, the high number of 5km stretches with no otter signs meant that the median was equal to zero in all seasons except Spring. Seasonal differences were, therefore, assessed using only those 5km stretches that produced otter signs and again the median number of both SIGN and SITE per 5km did not differ significantly between seasons (SIGN; $H_3 = 0.9$, NS; SITE; $H_3 = 1.1$, NS).

Table 3.3.1 Summary statistics of the number of otter spraints (SIGN) and the number of spraint sites (SITE) found during four seasonal surveys of forty 5km stretches of riverbank in the upper Tyne catchment between March 1993 and November 1994. Statistics for the combined sample are also provided determined from the total number and mean number of SIGN or SITE calculated from all four surveys.

	Number of SIGN per 5km stretch of riverbank				Number of SITE per 5km stretch of riverbank			
	Spring	Summer	Autumn	Winter	Spring	Summer	Autumn	Winter
Median	1.5	0	0	0	1.5	0	0	0
Range	107	58	22	55	68	46	18	35
Mean	8.5	5.5	2.8	5.8	5.6	3.9	2.2	4.3
Variance	339	135	31	127	134	73	19	63
Total	340	221	111	231	224	155	87	173

Table 3.3.2 Wilcoxon Signed Rank Tests (T) of the difference between the number of otter spraints (SIGN) and the number of spraint sites (SITE) per 5km stretch of riverbank. found during four seasonal surveys of forty 5km stretches of riverbank in the upper Tyne catchment between March 1993 and November 1994. ** denotes significance at $p<0.01$, * denotes significance at $p<0.05$

Season	T
Spring	-3.41**
Summer	-3.06**
Autumn	-2.36*
Winter	-3.18**

3.3.2 Pattern in the distribution of otter signs.

5km sample units

The high variance relative to the mean shown in Table 3.3.1 suggested that the distribution of both SIGN and SITE per 5km stretch was non-random in all seasons. This conclusion was confirmed by comparing the frequency distributions of these data (Figure 3.3.1) with a theoretical Poisson distribution using Kolmogorov-Smirnov goodness-of fit-tests (D statistic, Table 3.3.3). These showed that, in all cases, the distribution of SIGN and SITE differed significantly from random. These results, taken in conjunction with the substantial negative skew in the frequency distributions shown in Figure 3.3.1, suggested a high degree of clumping in the distributions of both SIGN and SITE in all seasons. This clumping was primarily caused by the higher proportion of 5km stretches with no otter signs than would be expected if they were randomly distributed throughout the sample. The analyses carried out so far showed that the distributions of both SIGN and SITE in the upper Tyne catchment in all seasons showed a clumped pattern. They did not however, give any indication of geographical patterns in the distribution of spraints and spraint sites. Figures 3.3.2 to 3.3.5 show that 5km

stretches in some parts of the catchment produced higher numbers of otter signs than others and that in many cases neighbouring 5km stretches produced similar numbers of otter signs suggesting geographical differences in spraint density. In particular, 5km stretches with high numbers of SIGN and SITE seem to occur more in the lower North Tyne and its western tributaries, the lower South Tyne and Allen and the two streams draining the hills above Kielder reservoir (Kielder and Deadwater Burns). If this is a true interpretation of these maps then it would be expected that the distribution of SIGN and SITE would exhibit spatial autocorrelation.

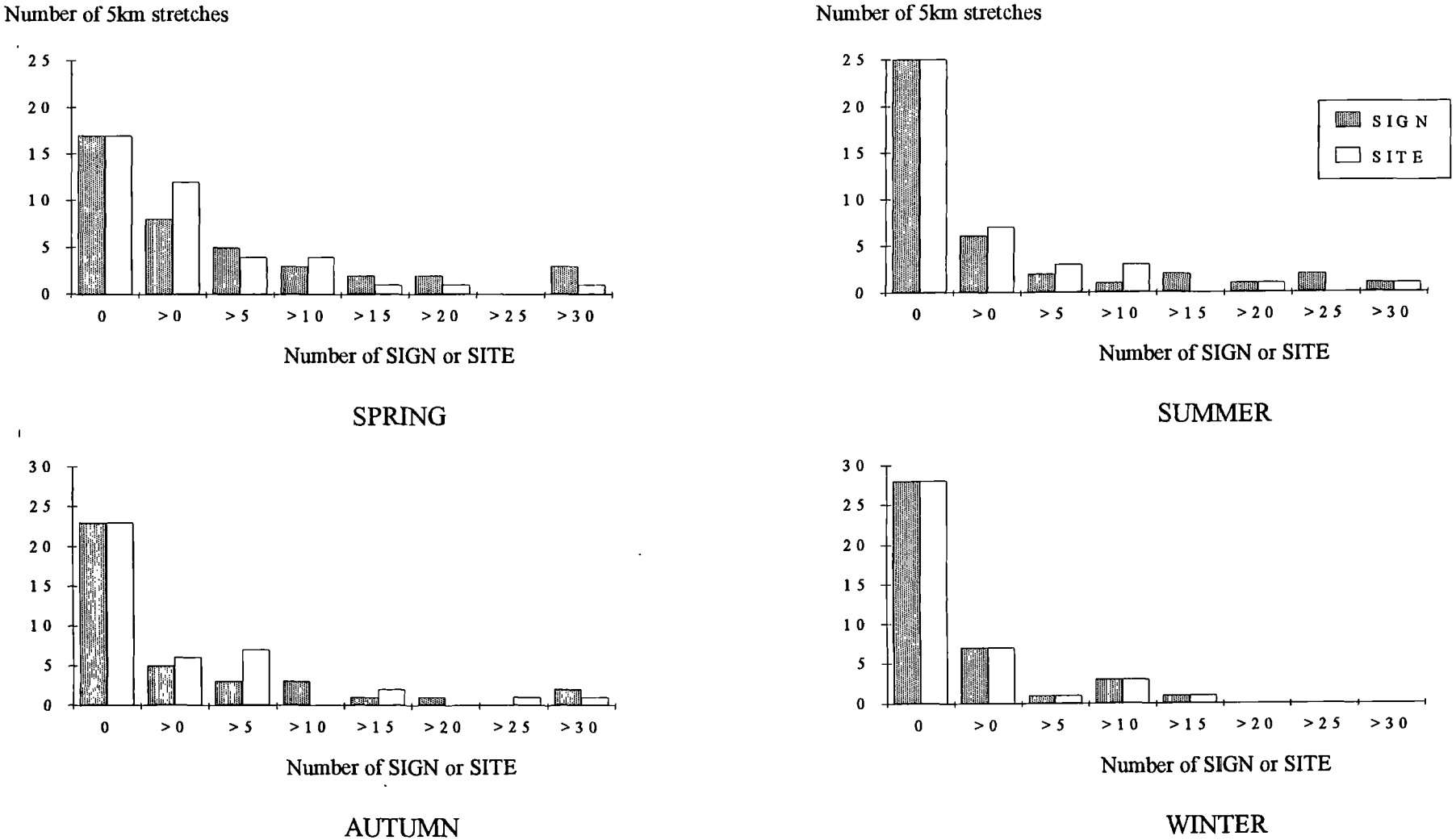


Figure 3.3.1: Frequency distributions, as the number of the forty 5km stretches of riverbank surveyed, for the number of SIGN and SITE found, in four seasonal surveys of the upper Tyne catchment between March 1993 and November 1994.

Table 3.3.3 Kolmogorov-Smirnov goodness-of-fit-tests (D statistic) results to determine whether the observed cumulative frequency distributions of the number of SIGN and SITE per 5km in each season differ significantly from an expected Poisson (random) distribution. * denotes significant at $p<0.05$, ** denotes significant at 0.01.

		D		$D_{[n, 0.05]}$	$D_{[n, 0.01]}$
Season	n	SIGN	SITE		
Spring	40	0.59**	0.52**	0.21	0.25
Summer	40	0.60**	0.62**	0.21	0.25
Winter	40	0.57**	0.56**	0.21	0.25
Autumn	40	0.64**	0.59**	0.21	0.25

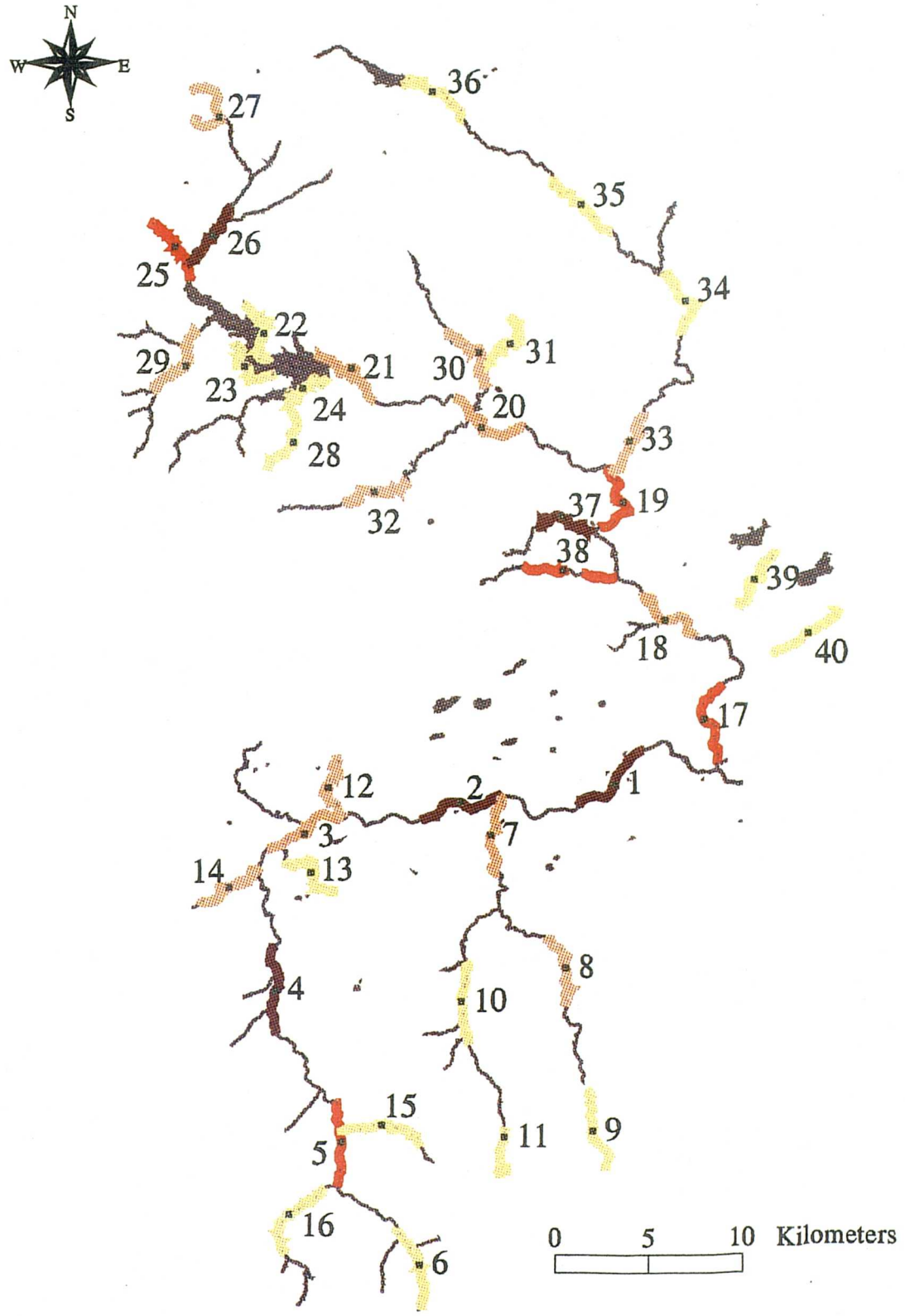


Figure 3.3.2: Map of forty 5km stretches of riverbank in the upper Tyne catchment showing the distribution of otter spraints in the Spring of 1993. Yellow lines represent 5km stretches which held no otter signs. Red lines indicate stretches with otter signs with the darkest shades indicating the highest densities of spraints.

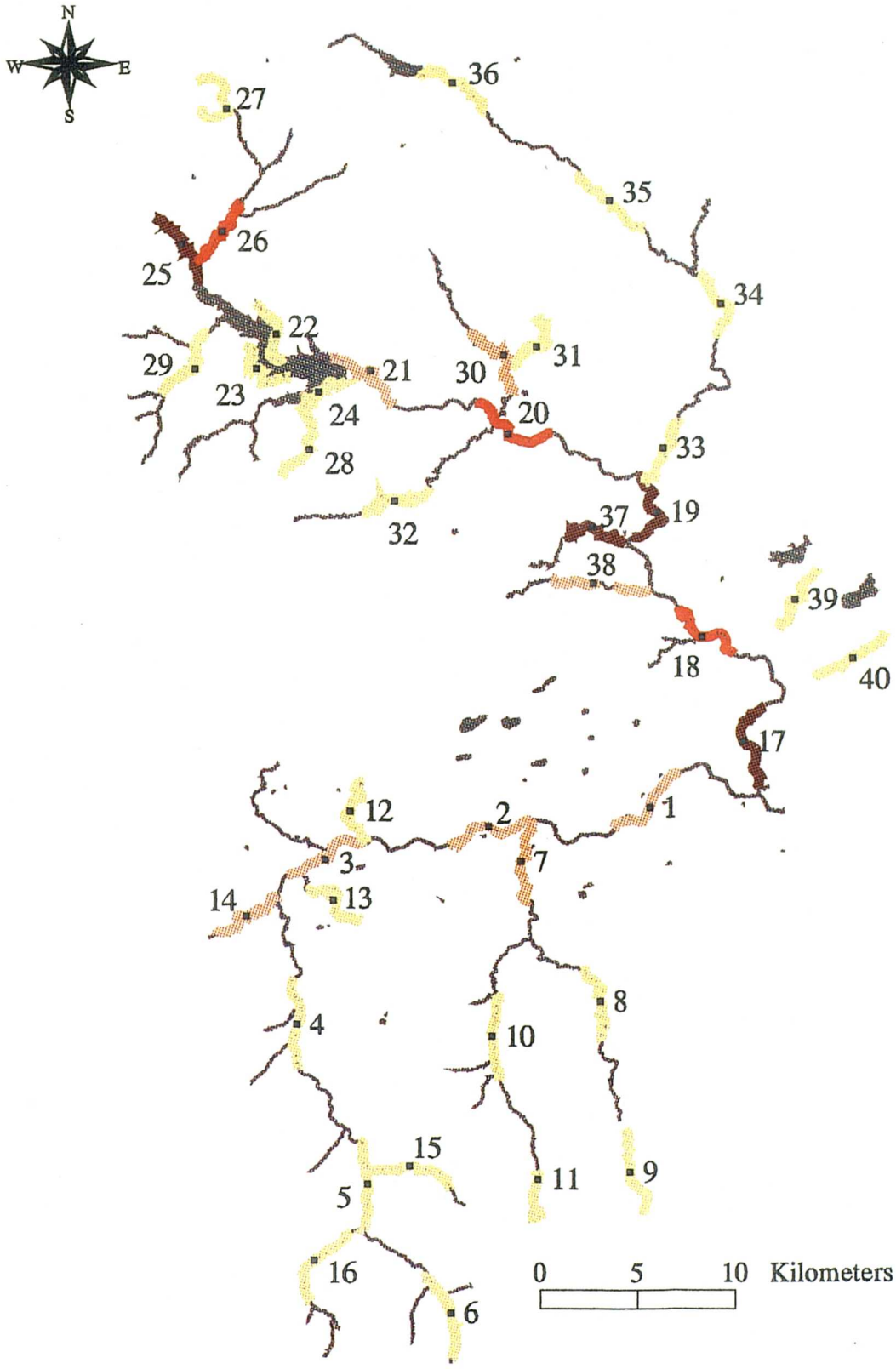


Figure 3.3.3: Map of forty 5km stretches of riverbank in the upper Tyne catchment showing the distribution of otter spraints in the Summer of 1993. Yellow lines represent 5km stretches which held no otter signs. Red lines indicate stretches with otter signs with the darkest shades indicating the highest densities of spraints.

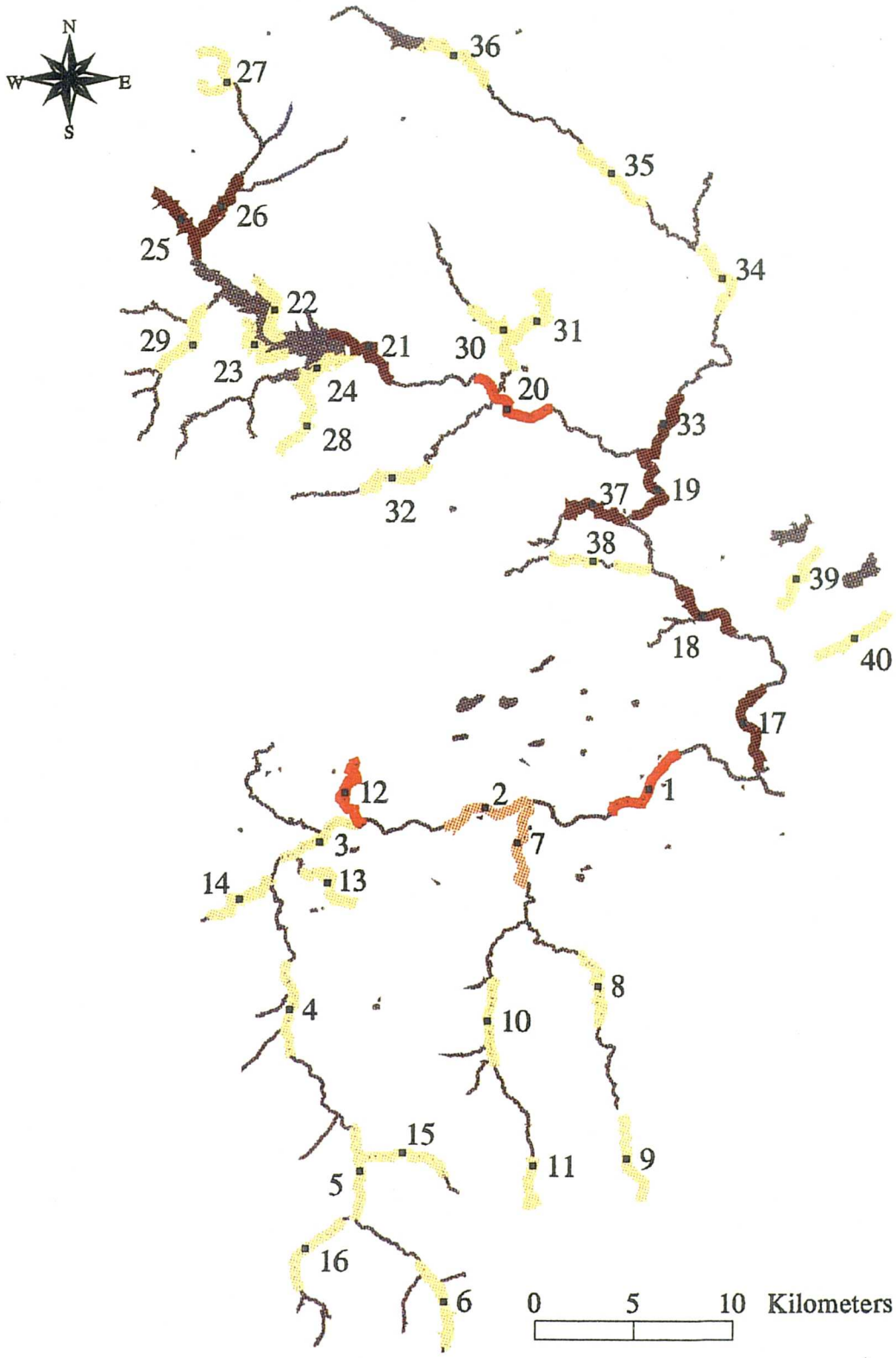


Figure 3.3.4: Map of forty 5km stretches of riverbank in the upper Tyne catchment showing the distribution of otter spraints in the Autumn of 1994. Yellow lines represent 5km stretches which held no otter signs. Red lines indicate stretches with otter signs with the darkest shades indicating the highest densities of spraints.

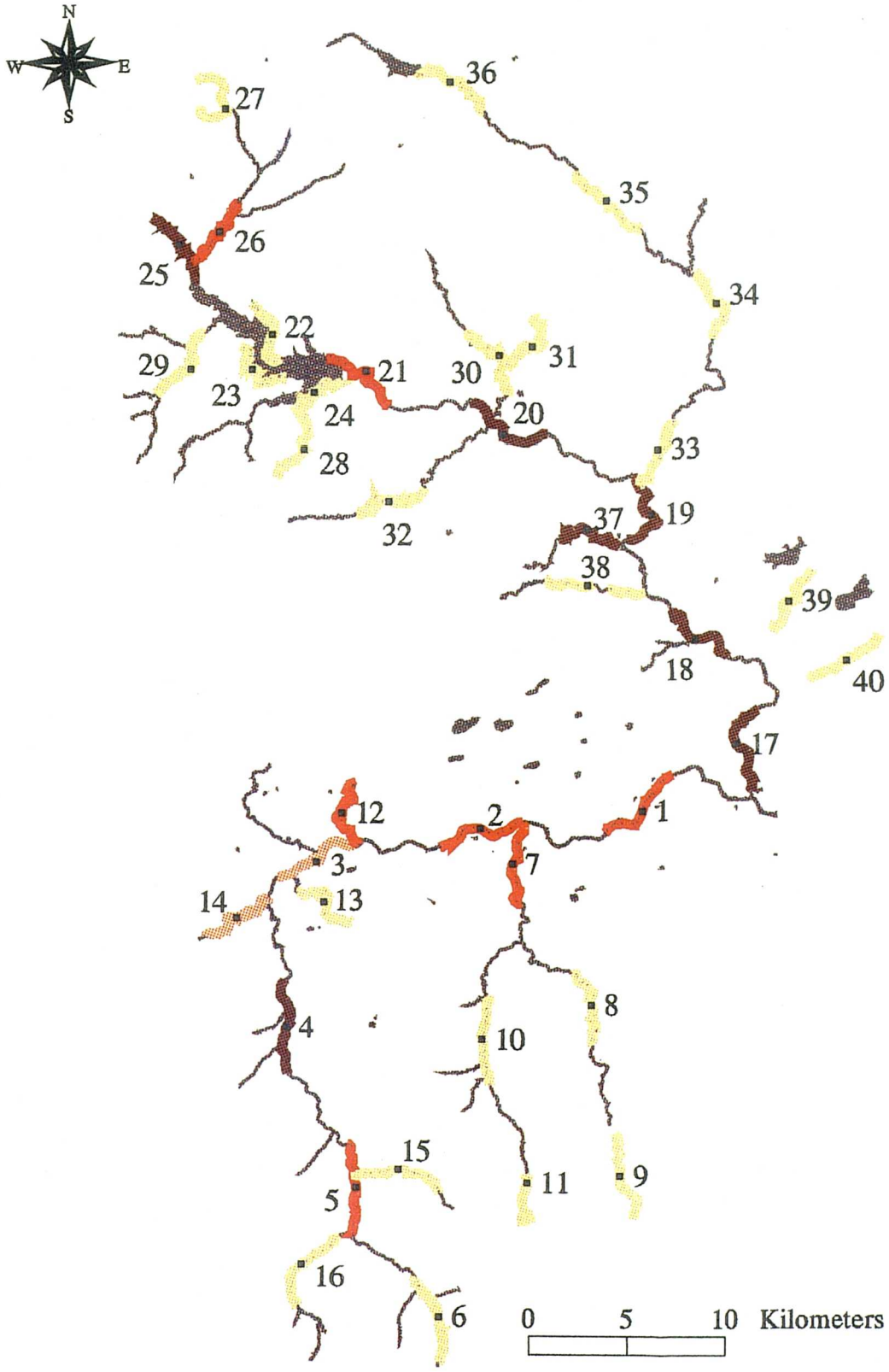
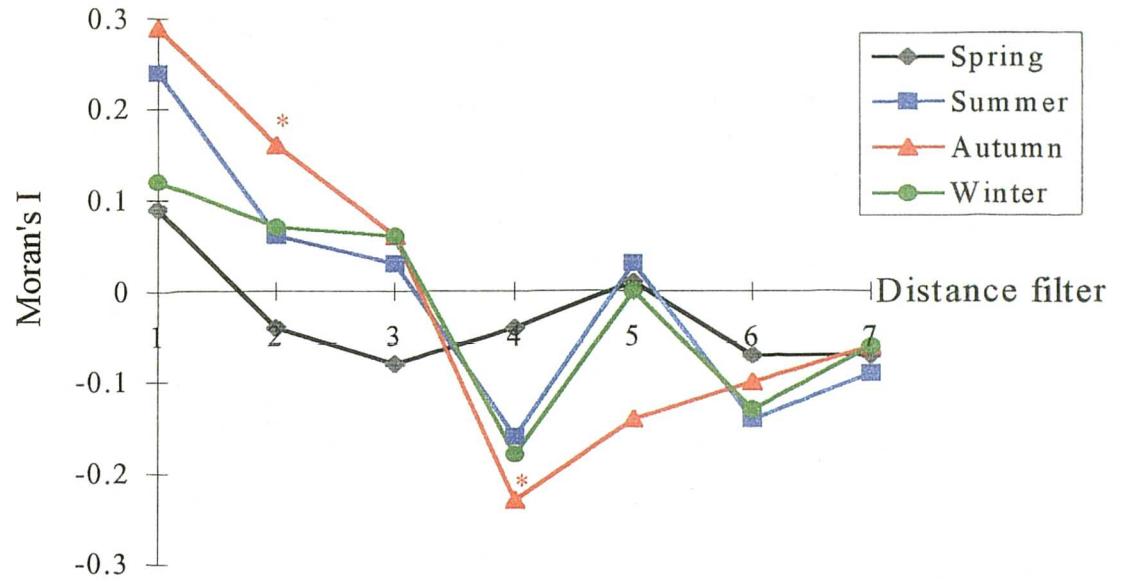


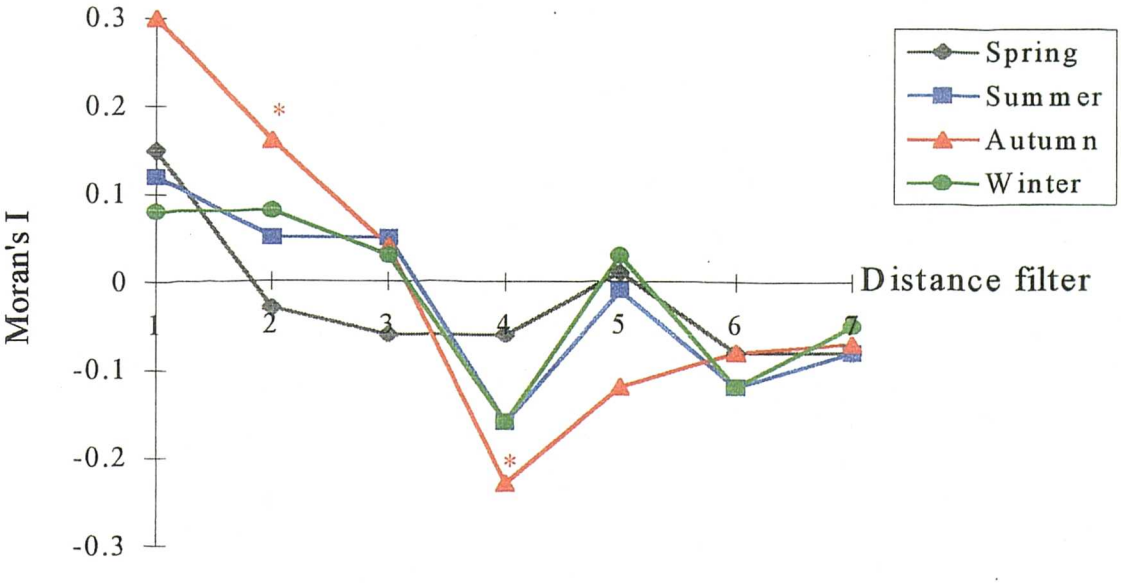
Figure 3.3.5: Map of forty 5km stretches of riverbank in the upper Tyne catchment showing the distribution of otter spraints in the Winter of 1994. Yellow lines represent 5km stretches which held no otter signs. Red lines indicate stretches with otter signs with the darkest shades indicating the highest densities of spraints.

Figure 3.3.6 shows Moran's I correlograms of spatial autocorrelation in the number of SIGN and SITE between 5km stretches of riverbank for each season using the distance filters outlined in section 3.2.2 (actual values are given in Table V.I in Appendix V). Values of Moran's I which were significant at $p < 0.01$ using the permutation approach (99 permutations) are marked with an asterisk. Both correlograms show that spatial autocorrelation was significant in the autumn only with peak positive autocorrelation at short separation distances (<20km) and peak negative autocorrelation at ≥30<40km.

However, Table 3.3.4 shows that in each season there were high numbers of 5km stretches with no otter signs and Figure 3.3.1 shows that the majority of stretches with otter signs produced only small numbers (<10) of SIGN or SITE. It is argued, therefore that the frequency distribution of the number of SIGN or SITE per 5km stretch is not continuous and would be better described as a dichotomous variable which consisted of 5km stretches with otter signs (PRESENT) and 5km stretches without otter signs (ABSENT). Under these circumstances the assessment of spatial autocorrelation using Moran's I is inappropriate and Join count statistics should be used instead (see Appendix IV).



SIGN



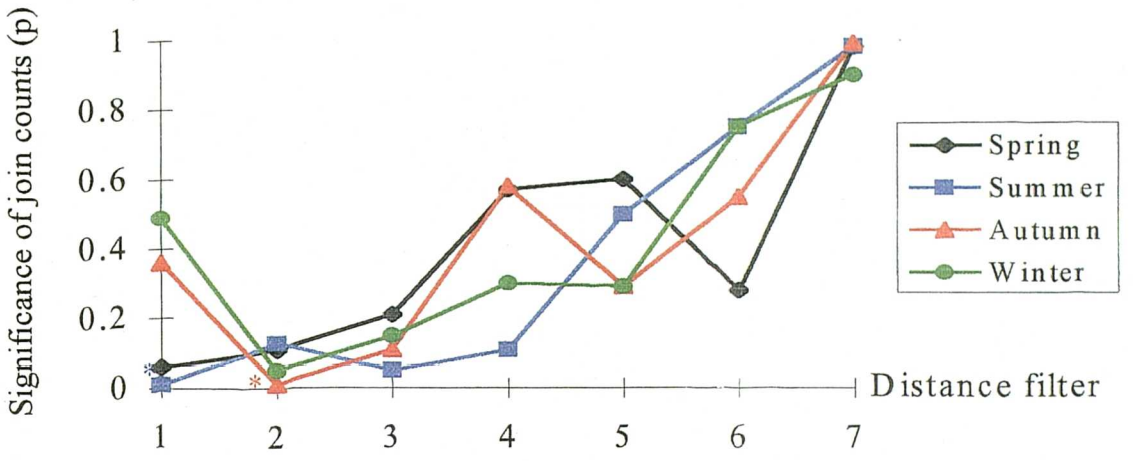
SITE

Figure 3.3.6 Moran's I correlograms showing spatial autocorrelation in the number of otter spraints (SIGN) or spraint sites (SITE) between 5km stretches of riverbank in the upper Tyne catchment at a series of separation distances (Distance filters). The distance filters used were 1 = ≥5<10km, 2 = ≥10<20km, 3 = ≥20<30km, 4 = ≥30<40km, 5 = ≥40<50km, 6 = ≥50<75km, 7 = ≥75<100km. Significant values ($p < 0.01$) are marked with an asterisk.

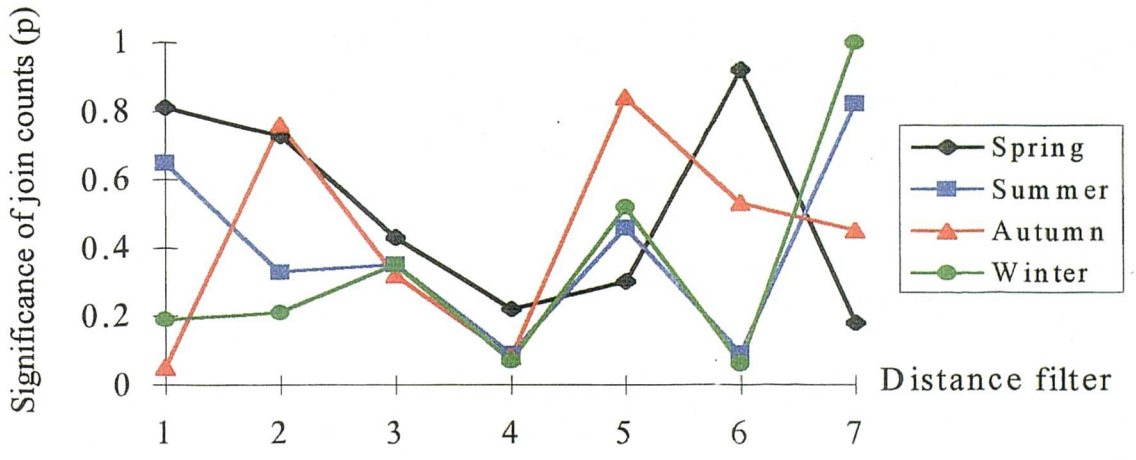
Table 3.3.4 Number of 5km stretches of riverbank with (PRESENT) and without (ABSENT) otter signs in each of four seasonal surveys of the upper Tyne catchment between March 1993 and November 1994.

	Spring	Summer	Autumn	Winter
PRESENT	23	15	13	16
ABSENT	17	25	27	24

Figure 3.3.7 shows the significance (p) values of join counts analysis based on the permutation approach outlined in Appendix IV for each distance filter for BB and BW joins (actual values are given in Table V.II in Appendix V). BB joins are between two contiguous 5km stretches with otter signs present (analogous to positive autocorrelation). BW joins are between two contiguous 5km stretches where one 5km stretch has otter signs present and its neighbour has no otter signs (analogous to negative autocorrelation). Statistically significant ($p < 0.01$) positive spatial autocorrelation was present between 5km stretches at short separation distances (<20km) in summer and autumn only.



BB counts



BW counts

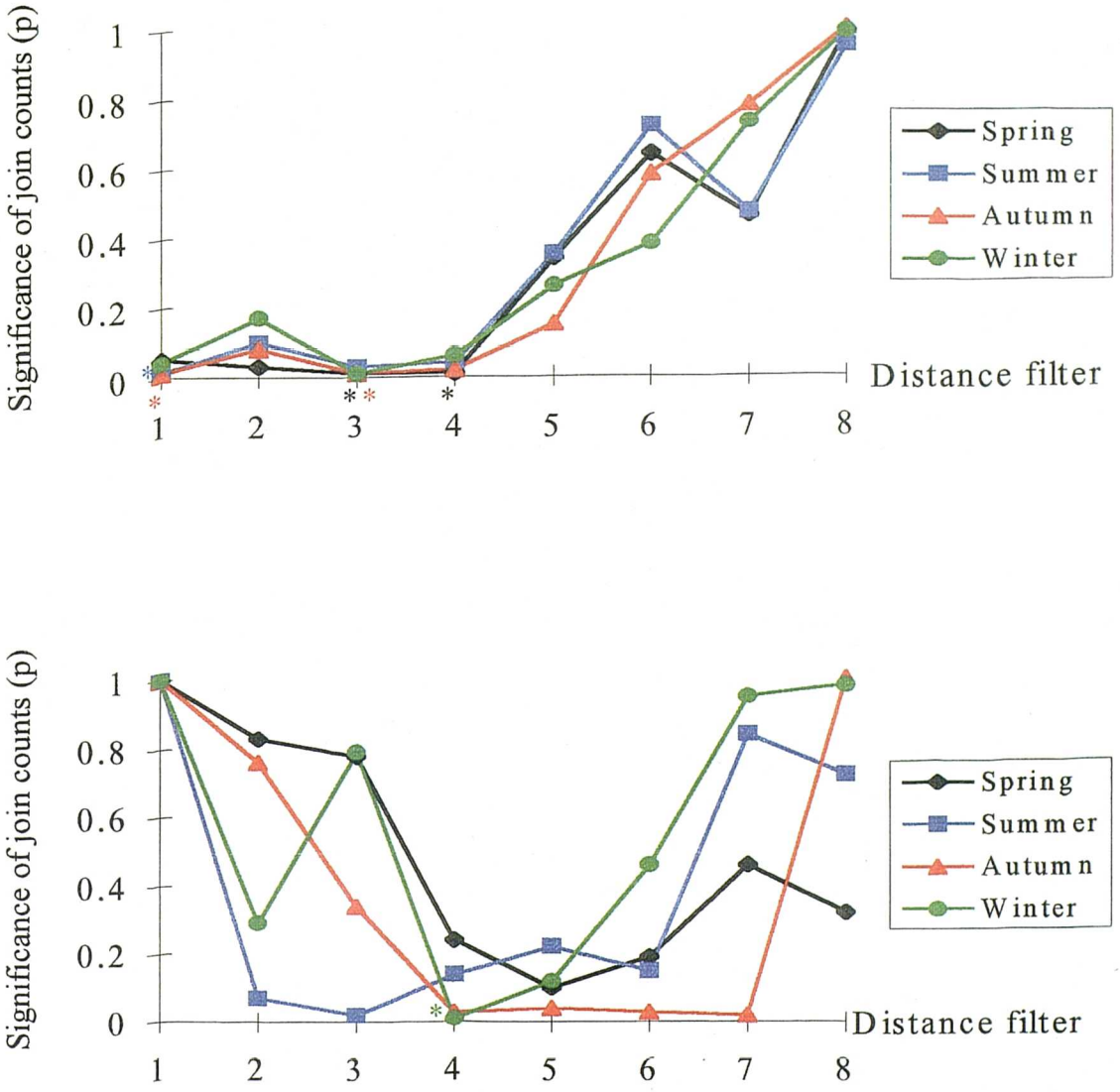
Figure 3.3.7 Join count correlograms showing the significance of spatial autocorrelation in the presence or absence of otter signs between 5km stretches of riverbank in the upper Tyne catchment at a series of separation distances (Distance filters). BB counts show spatial autocorrelation where otter signs are present in both 5km stretches (positive autocorrelation). BW counts show spatial autocorrelation wher otter signs are present in only one of the two neighbouring 5km stretches (negative autocorrelation). The distance filters used were 1 = ≥5<10km, 2 = ≥10<20km, 3 = ≥20<30km, 4 = ≥30<40km, 5 = ≥40<50km, 6 = ≥50<75km, 7 = ≥75<100km. Values which are significant at $p < 0.01$ are marked with an asterisk.

Spatial analysis using smaller sample unit sizes

The effect of reducing the sampling unit size to 2.5km, 1km, 600m or 200m respectively as outlined in the methods will be to further decrease the number of SIGN and SITE per sample unit. Therefore, it would be inappropriate to use statistical methods which rely on continuous distributions (e.g. comparisons with theoretical distributions or Moran's I statistics) to investigate patterns in the distribution of otters signs in the upper Tyne catchment. For this reason, join counts (see Appendix IV) were used in this section to determine the effect of changes in sample unit size on the patterns of spatial association between sample units.

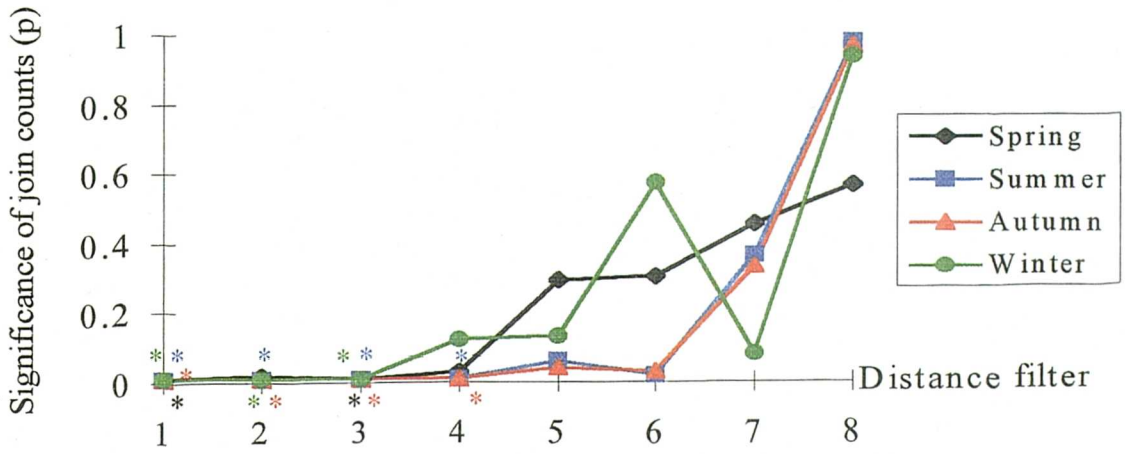
Figures 3.3.8 to 3.3.11 show Join count correlograms for each of the sample unit sizes (2.5km, 1km, 600m and 200m) using the distance filters outlined in section 3.2.2 (actual values are given in Tables V.III to V.VI in Appendix V). At the 2.5km and 1km sample unit sizes positive autocorrelation (BB counts) was significant at short separation distances (<20km) between sample units in some seasons as with the 5km sample unit size. At the 2.5km sample unit size negative spatial autocorrelation (BW counts) was significant in the winter only. However, at the 1km sample unit size negative spatial autocorrelation was present at distances of between 10 and 40km depending on the season. In the summer and autumn negative spatial autocorrelation between sample units was apparent at separation distances of up to 75km between stretches while in the winter and spring autocorrelation tailed off significantly at 50km between sample units. A similar pattern of spatial autocorrelation was observed using 600m sample unit sizes with positive spatial autocorrelation occurring at separation distances of up to 40km in summer and autumn. Negative spatial autocorrelation was apparent at separation distances of between 10 and 40km in all seasons and was still present in the summer and autumn at distances of 50km. At the 200m sample unit size positive spatial autocorrelation was present over most of the separation distances while negative autocorrelation was apparent at distances of 10 to 50km between stretches as was found for the other sample unit sizes. These results show that spatial clustering was present in the distribution of otter signs in the upper Tyne catchment. Positive spatial autocorrelation at short distances between sample units indicate that stretches within the same river or stream are more likely to be similar in the occurrence of otter signs. As this distance increases sample units become increasingly negatively autocorrelated which

may reflect differences between catchments. At the 1km and 600m sample unit sizes negative autocorrelation is apparent between sample units at considerable separation distances in the summer and autumn suggesting that differences between catchments are more pronounced in these seasons.

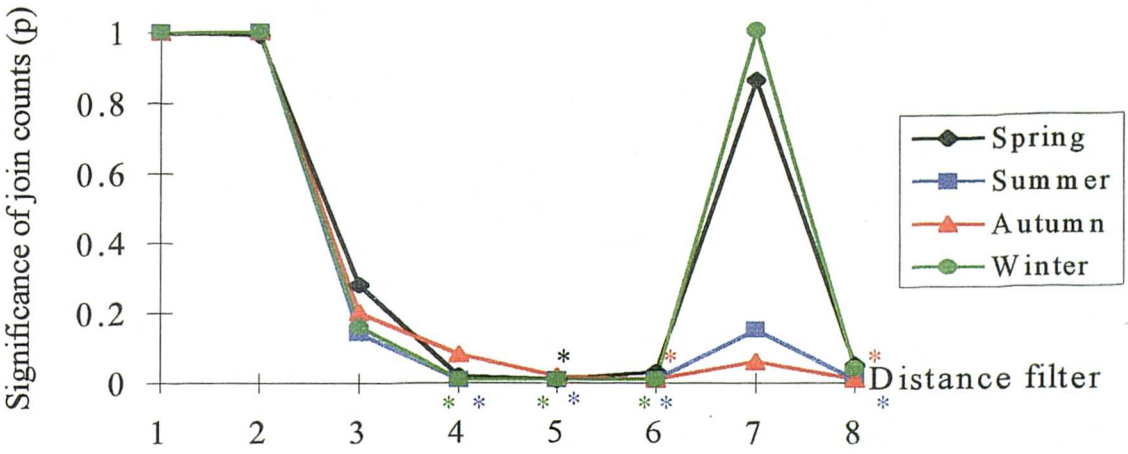


BW counts

Figure 3.3.8 Join count correlograms showing the significance of spatial autocorrelation in the presence or absence of otter signs between 2.5km stretches of riverbank in the upper Tyne catchment at a series of separation distances (Distance filters). BB counts show spatial autocorrelation where otter signs are present in both 2.5km stretches (positive autocorrelation). BW counts show spatial autocorrelation wher otter signs are present in only one of the two neighbouring 2.5km stretches (negative autocorrelation). The distance filters used were 1 = ≥2.3<2.7km, 2 = ≥5<10km 3 = ≥10<20km, 4 = ≥20<30km, 5 = ≥30<40km, 6 = ≥40<50km, 7 = ≥50<75km, 8 = ≥75<100km. Values which are significant at $p < 0.01$ are marked with an asterisk.

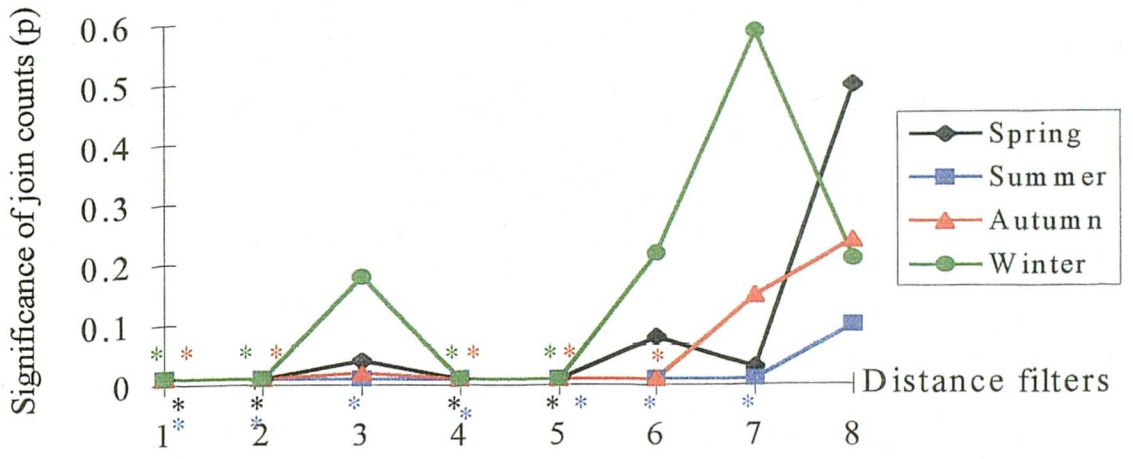


BB counts

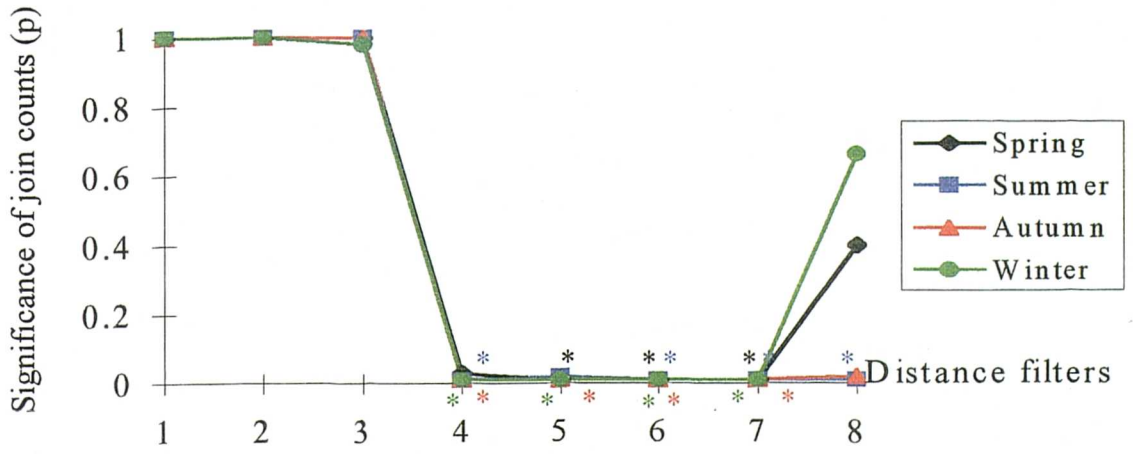


BW counts

Figure 3.3.9 Join count correlograms showing the significance of spatial autocorrelation in the presence or absence of otter signs between 1km stretches of riverbank in the upper Tyne catchment at a series of separation distances (Distance filters). BB counts show spatial autocorrelation where otter signs are present in both 1km stretches (positive autocorrelation). BW counts show spatial autocorrelation wher otter signs are present in only one of the two neighbouring 1km stretches (negative autocorrelation). The distance filters used were 1 = ≥0.8<1.2km, 2 = ≥2.8<3.2km 3 = ≥5<10km, 4 = ≥10<20km, 5 = ≥20<30km, 6 = ≥30<40km, 7 = ≥40<50km, 8 = ≥50<75km. Values which are significant at $p < 0.01$ are marked with an asterisk.

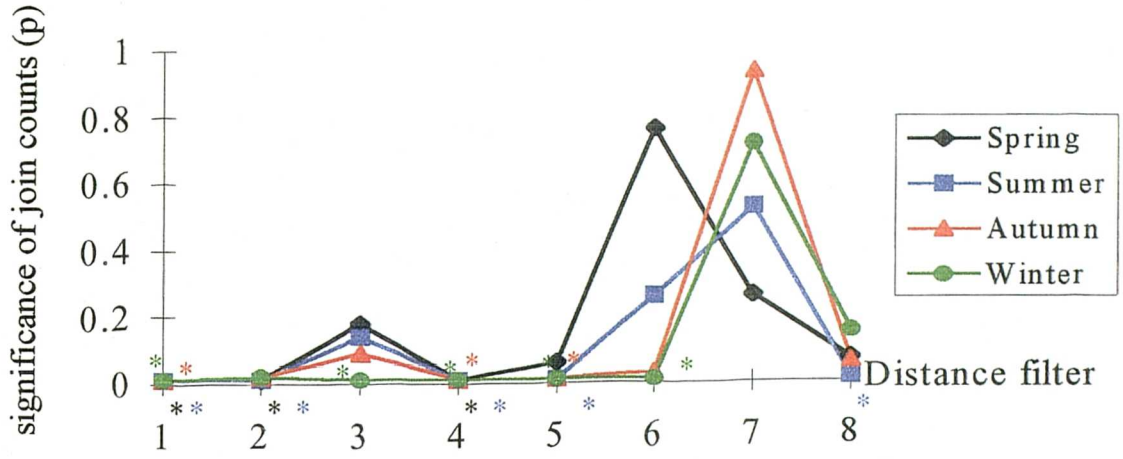


BB counts

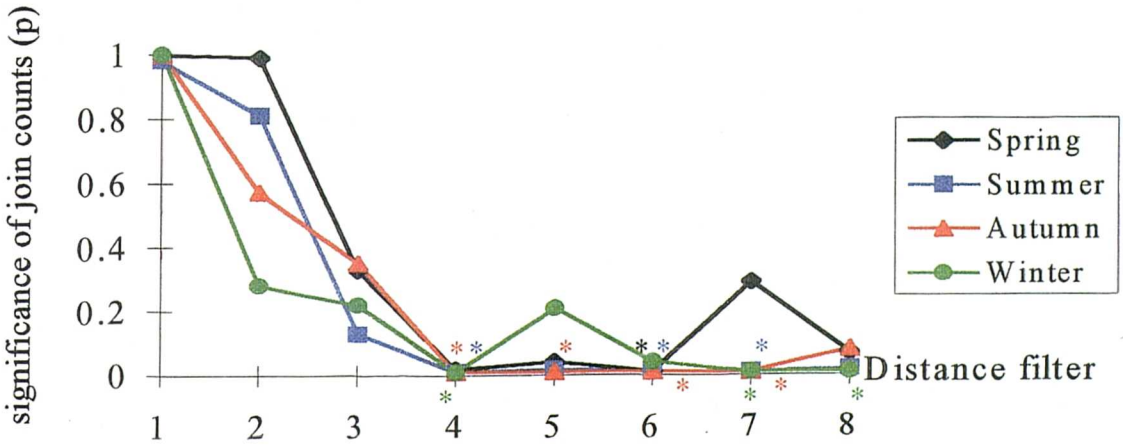


BW counts

Figure 3.3.10 Join count correlograms showing the significance of spatial autocorrelation in the presence or absence of otter signs between 600m stretches of riverbank in the upper Tyne catchment at a series of separation distances (Distance filters). BB counts show spatial autocorrelation where otter signs are present in both 600m stretches (positive autocorrelation). BW counts show spatial autocorrelation wher otter signs are present in only one of the two neighbouring 600m stretches (negative autocorrelation). The distance filters used were 1 = ≥1.1<1.3km, 2 = ≥2.3<2.5km 3 = ≥3.5<3.7km, 4 = ≥5<10km, 5 = ≥10<20km, 6 = ≥20<30km, 7 = ≥30<40km, 8 = ≥40<50km. Values which are significant at $p < 0.01$ are marked with an asterisk.



BB counts



BW counts

Figure 3.3.11 Join count correlograms showing the significance of spatial autocorrelation in the presence or absence of otter signs between 200m stretches of riverbank in the upper Tyne catchment at a series of separation distances (Distance filters). BB counts show spatial autocorrelation where otter signs are present in both 200m stretches (positive autocorrelation). BW counts show spatial autocorrelation wher otter signs are present in only one of the two neighbouring 200m stretches (negative autocorrelation). The distance filters used were 1 = ≥150<250m, 2 = ≥1.95<2.05km 3 = ≥3.95<4.05km, 4 = ≥5<10km, 5 = ≥10<20km, 6 = ≥20<30km, 7 = ≥30<40km, 8 = ≥40<50km. Values which are significant at $p < 0.01$ are marked with an asterisk.

3.3.3 Differences between North and South Tynes in the occurrence of otter signs

Table 3.3.5 shows that the proportions of stretches of riverbank with otter signs at the 5km and 2.5km sample unit sizes did not differ significantly between the North and South Tynes in all four seasons. At the other sample unit sizes however, the proportion of stretches with otter signs was significantly higher in the North Tyne than in the South Tyne in the Summer and Autumn.

Table 3.3.5 χ^2 tests of differences in the proportions of stretches of riverbank with otter signs in the North and South Tyne catchments (expressed as percentages) at 5km (n = 40), 2.5km (n = 70), 1km (n = 182), 600m (n = 304) and 200m (n= 498) sample unit sizes and during four seasonal surveys. One degree of freedom in all tests.

Sample unit size	Season	No. of stretches in catchment		stretches with otter signs (%)		χ^2	P
		South Tyne	North Tyne	South Tyne	North Tyne		
5km	Spring	16	24	56	54	<0.1	NS
	Summer	16	24	31	42	0.4	NS
	Autumn	16	24	25	38	2.3	NS
	Winter	16	24	50	33	1.1	NS
2.5km	Spring	28	42	50	45	2.3	NS
	Summer	28	42	39	50	0.3	NS
	Autumn	28	42	18	31	1.2	NS
	Winter	28	42	21	38	2.2	NS
1km	Spring	73	109	34	29	0.5	NS
	Summer	73	109	16	34	6.8	<0.01
	Autumn	73	109	12	27	6.3	<0.05
	Winter	73	109	29	32	0.2	NS
600m	Spring	120	184	28	26	0.1	NS
	Summer	120	184	10	26	12	<0.01
	Autumn	120	184	7	20	10	<0.01
	Winter	120	184	21	23	2.8	NS
200m	Spring	194	304	31	26	1.5	NS
	Summer	194	304	12	25	13	<0.01
	Autumn	194	304	5	19	21	<0.01
	Winter	194	304	18	26	4.5	NS

3.4 DISCUSSION

3.4.1 Patterns in the distribution of otter signs.

In this chapter it was clearly shown that there was a high degree of clumping in the distribution of otter signs (expressed as numbers of spraints or spraint sites per 5km stretch) in the upper Tyne catchment in all four seasons. Analysis of distribution maps showed that in the Summer and Autumn, otter signs were found mainly in the lower reaches of the South Tyne and throughout the main river stretches of the North Tyne. The lowest stretches of the Allen and the Rede (Autumn only) also produced high numbers of otter signs as did the two streams to the west of the lower North Tyne (the Houxty and Warks Burns). In the Spring and Winter otter signs were more widespread, occurring throughout the main river stretches of the North and South Tynes and in many of their tributaries. However, Walter (1993) argued that visual interpretation of maps was often influenced by the method of data representation. He showed that visual perception of maps was often inaccurate and that statistical methods such as spatial autocorrelation analysis provided a better estimate of regional variations. Spatial autocorrelation analysis of the presence or absence of otter signs in 5km and 2.5km sample unit sizes showed that there was very little spatial association in the distribution of otter signs. At the 1km, 600m and 200m sample unit sizes there was significant positive spatial association between sample units at separation distances of up to 20km. This demonstrated that stretches of riverbank in close geographical proximity were more likely to be similar in the presence or absence of otter signs. As the separation distance increased the degree of negative spatial association increased. It is argued that this was due to differences between lower and upper reaches of the catchments. It is also suggested that negative autocorrelation at the greatest distances between sample unit sizes was due to differences between the North and South Tyne catchments. The description of spatial pattern at the different sample unit sizes described in this study tended to confirm the conclusions of Wiens (1989) summarised in Table 3.1.1. At the 5km and 2.5km sample unit sizes presence or absence of otter signs was probably too coarse as a measure of the distribution of otter signs resulting in a loss of resolution. However, it was not possible to use spraint densities directly because of the small number of stretches surveyed. It would however, have been impractical to increase the

number of stretches due to the logistic constraints of surveying such large stretches of riverbank. These are some of problems of investigating ecological systems at broad scales as described in the Introduction to this chapter. As the size of the sample unit was decreased and consequently the number of samples increased significant patterns of spatial association became apparent. At these smaller sample unit sizes presence or absence of otter signs was a more accurate representation of the distribution of otter signs. These sample unit sizes may also be at the same scale as the underlying processes which cause spatial autocorrelation, such as patchiness in the distribution of resources. These findings fit the fine scale ecological systems outlined by Wiens (1989).

Jenkins & Burrows (1980) also demonstrated clumping in the distribution of otter spraints (in 2km sample units) in the river Dee, Aberdeenshire by comparison with a theoretical Poisson distribution. Bas, *et al.* (1981) demonstrated clumping in the distribution of otter spraints in the river Dee using the Index of Dispersion but this time 1km sampling units were used. However, these studies, and indeed all published studies of otter spraint distribution, took no account of spatial association in the distribution patterns yet, as was shown in the present study, spatial autocorrelation is prevalent in spraint distribution patterns.

Having shown that spatial autocorrelation is present in the pattern of distribution of otter signs in the upper Tyne catchment there is a need to determine the underlying processes which cause it. Spatial autocorrelation can be interpreted as a descriptive index, as in this chapter, measuring aspects of the way objects are distributed in space, but at the same time it can be seen as a causal process measuring the effect that something can have on its neighbours (Goodchild, 1986). Spatial autocorrelation in the distribution of an attribute variable may be caused by two processes. First, the value of the attribute at one location may have a direct effect on its neighbours. For example, territorial or competitive behaviour in a species may result in neighbouring individuals being in conflict resulting in some form of spacing out between individuals which might manifest itself as negative spatial autocorrelation. Alternatively, reproductive or social behaviour may mean that individuals are attracted to each other resulting in neighbouring individuals being positively autocorrelated. In this study, it is obviously not the behaviour of the spraints themselves but the behaviour of the otters producing those spraints which may cause spatial autocorrelation in the distribution of spraints. Erlinge

(1968a) showed that intense sprainting occurred in the "meeting zones" of otters coming from different areas and argued that this was the result of territorial behaviour. If this is the case we might expect sample sites in these "meeting zones" to exhibit positive spatial autocorrelation with sprainting by one individual stimulating sprainting by others. However, Jenkins (1980) demonstrated territoriality in otters on the Dinnet lochs, Aberdeenshire, only during severe winters and low otter densities. He argued that Erlinge's (1968a) findings may be typical of low densities of otters, whereas in milder conditions autumn-born young may survive with the pattern of spatial territoriality breaking down at higher densities. Green, Green & Jefferies (1984) used isotopic labelling to mark the spraints of two radio-tracked female otters in the River Earn catchment in Perthshire. They showed that an individual's sprainting behaviour increased in the presence of other individuals and that, in females at least, sprainting was more frequent at activity centres rather than boundaries. Therefore, it is probable that the behaviour of individual otters will in part determine patterns in the number and distribution of otter signs in a particular area.

A second process which may cause spatial autocorrelation in the pattern of distribution of a species is that this distribution is caused by an underlying parameter which is also spatially distributed. For example, the presence of a species in a series of sampling units may exhibit clustering (and therefore positive autocorrelation) in part of the geographical extent of a study area. This clustering may be caused by the spatial distribution of the species' preferred habitat type which may also be clustered in these areas. In a number of studies of habitat utilisation by otters, it has been argued that the distribution of otter signs is related to the distribution of habitat features such as the availability of woodland or holt sites (see Mason & Macdonald, 1987). Kruuk (1992) argued that otters sprainted to signal priority of use of resources to other otters. He demonstrated that sprainting by otters in Shetland was associated with the start of feeding bouts as well as with the utilisation of freshwater and holts. Therefore, it might be expected that the distribution of these resources may determine the distribution of spraints and, if these resources are not uniformly distributed in space, would produce clustering (spatial autocorrelation) in the pattern of that spraint distribution.

The two processes which generate spatial autocorrelation were described by Cliff & Ord (1981) as interactive and reactive respectively. It would be extremely difficult to

determine interactive effects on the pattern of spraint distribution without detailed observations of individual otters which would be impractical on a catchment-wide scale because of logistic constraints. However, the relationship between environmental parameters and spraint distributions (i.e. reactive effects) can be determined more easily. Goodchild (1986) argued that if the processes which generated the pattern in the spatial distribution of the attribute (in this case the distribution of spraints) were solely reactive then, if all the causative factors can be found and modelled, the residuals from this model will be completely lacking in spatial autocorrelation. If on the other hand, autocorrelation is present then the pattern may be generated by interactive factors, other reactive factors or a combination of both. The work described in the remainder of this thesis aims to find those reactive factors which may be associated with the distribution of otter signs and determine whether reactive effects are solely responsible for this distribution.

The presence of spatial autocorrelation in the distribution of an attribute variable brings with it a statistical problem. That is, because the value at any one location can be partially predicted by the values at neighbouring locations, these values are not stochastically independent of one another (Legendre, 1993). This then impairs our ability to carry out standard statistical tests of hypotheses. In many cases positive autocorrelation results in computed statistics being declared significant too often under the null hypothesis. In addition, because it is possible to partially predict the value of a location from the value of its neighbours, each new observation does not carry with it a full degree of freedom since in classical statistics one degree of freedom is provided by each independent observation. Several solutions are available to cope with spatially autocorrelated data. The first is to remove its effect by randomly removing samples until spatial independence is achieved. This results in a loss of information which would be considerable in this study where spatial autocorrelation is present at a number of different spatial scales. Spatial dependence could also be filtered out using various methods described by Cliff & Ord (1981). However, the approach preferred by Legendre (1993) was to modify the statistical method in order to take spatial autocorrelation into account A number of statistical methods are now available to do this (see review in Legendre, 1993). In the remainder of this thesis spatially corrected statistics will be used where appropriate.

3.4.2 Seasonality in the distribution of otter signs.

The highest numbers of otter spraints in the upper Tyne catchment were found in the Spring and Winter surveys. However, no significant differences in the average number of otter signs per 5km stretch were found between seasons primarily due to the high number of 5km stretches with no otter signs. There were however, temporal differences in the geographical pattern of spraint distribution with otter signs being widespread throughout the catchment in the Spring and Winter surveys and restricted to the North Tyne and lower reaches of the South Tyne in Summer and Autumn surveys. Erlinge (1967a) showed seasonality in the behaviour of otters in Sweden. In the Spring otters were highly active, dispersing and reoccupying areas which were abandoned as feeding grounds in winter. In the Summer however, their behaviour changed, with otters seeking suitable haunts and remaining within restricted areas. Females with cubs would often stay in the same place for many weeks while adult dog otters would cover their home ranges, although even their travels were less extensive. Sprainting activity continued, in some places intensively, but usually in secluded places. Towards the end of summer, activity gradually increased, reaching a peak in Autumn and Winter with some otters travelling considerable distances to find suitable haunts. This pattern of more widespread activity in the Spring and Winter was consistent with the distribution of otter signs in the upper Tyne catchment. Jenkins & Burrows (1980) also demonstrated peaks in spraint numbers in Spring and Winter and troughs in the Summer and Autumn, tentatively suggesting that this was related to the presence of more otter families in Spring and fewer in the Summer. Similar seasonal fluctuations in spraint numbers were observed by Macdonald and Mason (1987) working on the River Severn in Wales. They argued that this was due to the development or reinforcement of dominance relationships when young otters became independent. Kruuk (1992) also demonstrated seasonality in sprainting behaviour in otters in Shetland with peak sprainting rates in the winter. He argued that, in Shetland, this peak was just prior to the mating season suggesting a sexual function. However, in other areas of Britain mating is not seasonal (Mason & Macdonald, 1986) therefore it was unlikely that seasonal changes in sprainting behaviour were the result of sexual activity. Kruuk (1992) also showed that spraints were not deposited at territorial boundaries suggesting that sprainting was not related to territoriality although Erlinge (1968a) had shown increased sprainting at territorial boundaries in Sweden. These differences may be due to differences in population

densities, as discussed earlier. Kruuk (1992) argued that, as spraints were short-lived on the coasts of Shetland (being below the tide-line) and as sprainting was seasonal and sprainting rates were the same regardless of sex or status, their function was to signal precedence of use of resources, in this case, the use of feeding patches. However, this may not fully explain the function of otter spraints in freshwater environments, where spraints are often long-lived and regularly re-marked (Jenkins & Burrows, 1980). Therefore, the exact significance of seasonal changes in sprainting behaviour is unknown but must be taken into account when considering the factors that determine patterns in the distribution of otter signs.

4 THE DIET OF OTTERS IN THE UPPER TYNE CATCHMENT IN RELATION TO PREY ABUNDANCE

4.1 INTRODUCTION

One factor that may influence the distribution of otters and consequently their sprainting activity in particular areas is the distribution of their prey. Therefore, prior to investigating the relationship between the distribution of otter signs and environmental variables in the upper Tyne catchment it was necessary to determine what that prey was. There are two main methods used for the determination of carnivore diets - the analysis of gut contents or of faecal material (Reynolds & Aebischer, 1991). In studying the diet of otters, faecal analysis is used most widely due to the ease of collection of otter spraints and because the method does not involve destructive sampling. The apparent ease of assessing diet from spraints has ensured that this is an aspect of otter ecology that has received considerable attention with a sizeable literature on the subject (see, for example, reviews in Chanin, 1985 and Mason & Macdonald, 1986).

4.1.1 Types of prey taken.

Almost all studies have shown otters to be predominantly piscivorous with salmonids and eels (*Anguilla anguilla*) being the main prey species in riparian habitats and mammals and birds forming only a minor component of the diet (see Table 4.1.1). Amphibians formed a small though seasonally important component in some studies (Erlinge, 1967b and Weber, 1990). Invertebrates in faeces were usually assumed to be the result of secondary ingestion although some studies did show that otters actively preyed on large invertebrates such as *Dytiscus* spp. (Jenkins *et. al.*, 1979; Wise *et. al.*, 1981; Foster & Turner, 1991 Kozena *et al.*, 1992 and Carss & Parkinson, 1996) and the importance of crayfish (*Austropotamobius pallipes*, *Pacifastacus leniusculus*, *Procambarus clarki*) in the diet was demonstrated in a number of studies (McFadden & Fairley, 1984; Adrian & Delibes, 1987; Delibes and Adrian, 1987 and Thom, 1989).

TABLE 4.1.1 Summary of studies of the diet of the otter (*Lutra lutra*) showing the main prey types found in faecal analysis. F/W = freshwater; FOcc. = Frequency of occurrence, Bulk = bulk estimate.

LOCATION & DATE	Lake Sovdesjon Sweden 1960	Lake Snogeholmssjon Sweden 1960	Lake Ellestadssjon Sweden 1960	Snogeholmsan Sweden 1960	Ellestadsan Sweden 1960	Klingavalsan Sweden 1960	Dinnet Lochs Aberdeenshire		
HABITAT TYPE	F/W lake	F/W lake	F/W lake	F/W stream	F/W stream	F/W stream	F/W lake	F/W lake	F/W lake
RESULT FORMAT	FOcc. (%)	FOcc. (%)	FOcc. (%)	FOcc. (%)	FOcc. (%)	FOcc. (%)	Focc.(%)	Bulk 51-75 (%)	Bulk 76-100 (%)
Cyprinids	44	54	45	53	53	6	-	-	-
Percids	25	13	22	16	15	4	46	2	4
Pike (*Esox lucius*)	6	7	10	10	9	8	33	0.8	0.8
Salmonids	-	-	-	-	-	-	9	0.1	0.3
Eel (*Anguilla anguilla*)	3	6	4	2	3	0.4	86	12	62
Burbot (*Lota lota*)	0.7	0.3	-	2	0.5	6	-	-	-
Bullhead (*Cottis gobio*)	-	-	-	-	-	-	-	-	-
Stickleback (*Gasterosteus* sp.)	0.4	0.3	-	0.2	-	5	-	-	-
Unidentified fish	2	0.8	0.2	0.9	0.2	0.9	-	-	-
Crayfish	10	11	7	5	9	36	-	-	-
Amphibians	1.7	0.2	2	2	0.8	30	21	0.3	0.7
Birds	5.7	6	9	7	8	3	20	0.1	6
Mammals	0.2	0.2	0.6	0.2	0.2	0.9	21	1	2
Insects	1.6	1.8	1	0.6	0.7	0.7	-	-	-
Molluscs	0.5	0.5	-	0.1	0.1	0.1	-	-	-
REFERENCE	Erlinge (1967b)	Erlinge (1967b)	Erlinge (1967b)	Erlinge (1967b)	Erlinge (1967b)	Erlinge (1967b)	Jenkins *et al.* (1979)	Jenkins *et al.* (1979)	Jenkins *et al.* (1979)

TABLE 4.1.1 continued.

LOCATION & DATE	River Dee Aberdeenshire			Slapton Ley Devon	River Webburn Devon	River Clare Ireland		Burn of Sheeoch Aberdeenshire	Polana PLR Czechoslovakia
HABITAT TYPE	F/W river	F/W river	F/W river	F/W lake	F/W River	F/W river	F/W river	F/W river	F/W river
RESULT FORMAT	FOcc. (%)	Bulk 51-75 (%)	Bulk 76-100 (%)	Bulk (%)	Bulk (%)	Focc. (%)	Bulk (%)	Focc. (%)	F. occ (%)
Cyprinids	-	-	-	45	-	-	-	11	0.8
Percids	0.7	0.0	0.0	10	-	22	5	-	11
Pike (*Esox lucius*)	1	0.0	0.0	8	-	9	4	9	-
Salmonids :Overall	80	2	79	-	59	14	5		61
>30cm								79	
Small								51	
Eel (*Anguilla anguilla*)	23	2	17	28	16	14	5	-	-
Burbot (*Lota lota*)	-	-	-	-	-	-	-	-	-
Bullhead (*Cottis* spp.)	-	-	-	-	7	-	-	-	43
Stickleback (*Gasterosteus* sp.)	-	-	-	1	-	18	3	-	-
Unidentified fish	-	-	-	-	-	15	4	3	1.5
Crayfish	-	-	-	-	-	66	60	-	-
Amphibians	5	0.0	2	1	6	17	7	11	44
Birds	2	0.0	0.6	7	2	7	3	-	2
Mammals	16	1	9	4	8	1	0.8	3	7
Insects	-	-	-	3	4	22	2	-	-
Molluscs	-	-	-	-	-	-	-	-	-
REFERENCE	Jenkins & Harper (1980)	Jenkins & Harper (1980)	Jenkins & Harper (1980).	Wise *et al.* (1981)	Wise *et al.* (1981)	McFaden & Fairley (1984)	McFaden & Fairley (1984)	Carss, *et al.* (1990)	Kozena *et al.* (1992)

4.1.2 The reliability of spraint analysis for determining dietary composition

All of these studies argued that spraint analysis, with results presented as 'percentage frequency' or 'relative frequency', provided a simple method that yielded good estimates of the relative importance of items in the diet. This conclusion was based on the results from feeding trials with captive otters conducted by Erlinge (1968b) and Rowe-Rowe (1977). However, as Carss & Parkinson (1996) pointed out, these two studies and the majority of other spraint analysis studies did not provide confidence limits for their estimates of the proportions of different prey species in the diet. Where 95% confidence limits had been calculated (Jenkins *et. al.*, 1979; Jenkins & Harper, 1980) they were so wide that any statistical differences in prey composition between locations or seasons were highly suspect. In their feeding trials with captive otters, Carss & Parkinson (1996) showed that there was a strong positive correlation between both percentage frequency or relative frequency of prey items in spraints and the proportions of prey groups fed to otters. However, they then showed that both percentage and relative frequencies over-estimated the true proportions of prey in the diet by a factor of between 5% and 2900% while the true proportions of some prey groups were under-estimated by a factor of between 12.5% and 50%. They concluded that spraint analysis could indicate the relative rank of the different prey items in the diet but could not accurately assess the exact proportions of prey groups in the diet.

In addition to these findings they showed that one of the basic assumptions of determining diet from "frequency of occurrence methods", that is, that each occurrence of a prey species in a spraint represented a different individual item, was demonstrably invalid since the remains of up to seven similarly sized fish were recorded in some spraints and the remains of a single prey item were found in up to 14 different spraints. This demonstrated that the proportions of some prey groups would be over-estimated if sequentially deposited spraints were collected regularly from frequently used sites. They also found that most remains of a particular prey item passed through the otters' digestive system within 24h and that all remains were expelled within 3 days. They concluded that spraints collected from a particular area would not necessarily reflect the prey caught in that area. This finding may therefore reduce the validity of comparing geographical differences in the diet of otters if spraints are collected in closely associated habitats (e.g. Beja, 1991). Carss & Parkinson (1996) also demonstrated that many fish

and invertebrate remains were the result of secondary ingestion from the stomachs of prey fish and that these could not be distinguished from the remains of fish that were the result of primary ingestion. They argued that this may result in over-estimation of small fish species in areas with piscivorous fish. They suggested that this may also be important in areas where brown trout (*Salmo trutta*) were the main prey species since these may sometimes become piscivorous (L'Abee-Lund, Langeland & Seagrov, 1992). The effect of different time intervals between spraint collection tended to increase the coefficient of variation of percentage frequency estimates in Carss & Parkinson's (1996) feeding trials particularly for rare prey groups but the rank order of prey proportions in the diet remained the same. They also demonstrated that taking sub-samples of spraints (to simulate incomplete collection or to allow for the proportion of spraints that otters defecate directly into the water (Kruuk, 1992)) led to variations in the proportions of prey groups estimated in the diet of only 1% with the biggest effect being observed for the rarest prey groups. This demonstrated that reduced sample sizes and longer periods between sample collections should not drastically reduce the accuracy of the estimates of prey proportions in the diet particularly in the light of the other more significant errors associated with spraint analysis methods.

4.1.3 The reliability of spraint analysis for determining prey size selection

The undigested prey remains in otter spraints have also been used to assess the size of prey consumed by otters. Wise (1978, 1980) calculated a series of correlations between fish length and the centrum length of individual vertebrae for a number of fish species. She showed that, in feeding trials with captive mink *Mustela vison,* regression equations could be used to estimate the size of fish prey from the length of vertebrae collected from scats. These equations have since been used in a large number of studies in many countries to assess prey size selectivity by both otters and mink (see Table 4.1.2). However, Carss & Elston (1996) showed that the 'mean' equations described by Wise (1978, 1980) consistently underestimated the true fish length and estimated weight of both trout and eel with errors varying between 3.2% and 19.0% of true fish length and between 9.0 and 50.0% of estimated weight. Feltham & Marquiss (1989) showed that salmonid atlas bones (first vertebrae) could be used to accurately distinguish between trout and salmon (*Salmo salar*). Carss & Elston (1996) conducted feeding trials with captive otters to determine the accuracy of using these bones and eel thoracic vertebrae

TABLE 4.1.2 Summary of studies of the diet of the otter (*Lutra lutra*) showing sizes of the main prey types found in otter spraints. Fish fork-snout lengths calculated from measurements of antero-caudal vertebrae (Wise, 1978, 1980). Crayfish carapace lengths calculated by measurement of uropod endopodites (all values in centimetres).

LOCATION	Dinnet lochs Aberdeen	Dinnet lochs Aberdeen	River Dee Aberdeen	Slapton Ley Devon	River Webburn Devon	River Clare Ireland
HABITAT TYPE	F/W lake	F/W lake	F/W river	F/W lake	F/W river	F/W river
Eel (*Anguilla anguilla*)	22-42	23-32	23-32	25-30	25-30	30-35
Pike (*Esox lucius*)	13-21	12-19	-	50-60	-	10-20
Salmonids	9.5-17	7-12	7-12	-	6-9	6-9
Perch (*Perca fluviatilis*)	6.6-12	5.5-5.9	5.5-5.9	6-9	-	-
Roach (*Rutilis rutilis*)	-	-	-	9-12	-	-
Crayfish	-	-	-	-	-	3.8-4.9
REFERENCE	Jenkins *et al.* (1979)	Jenkins & Harper (1980)	Jenkins & Harper (1980)	Wise *et al.* (1981)	Wise *et al.* (1981)	McFaden & Fairley (1984)

to estimate prey species composition, number of fish and size of salmonids and eels in the diet of otters. They showed that the total proportion of ingested salmonid atlas bones recovered from spraints was only 44%, varying from 30% to 77% between trials. This level of recovery suggested that minimum number estimates of salmonids ingested could not be calculated from faecal remains. Carss & Elston (1996) also found that both salmonid atlas bones and eel thoracic vertebrae were subject to size-related differential recovery with atlas bones of larger salmonids over-represented and smaller ones under-represented. For eels the opposite was the case, with the largest proportions of eel vertebrae recorded from the smaller size classes and few from the largest eels. These findings cast doubt on the conclusions of Kruuk *et al.* (1993) that otters ignored smaller salmonids. Carss & Elston (1996) also suggested that the occurrence of smaller salmonids and larger eels may have been under-estimated in many previous studies. They produced simple equations to account for the size-related differential recovery of salmonid atlas bones and eel thoracic vertebrae and argued that it was likely that other fish species may also yield differential bone recoveries in otter diets. It was suggested that the relatively large numbers of otters in captive breeding programmes could be used to model bone recovery for other fish species and for mammal and amphibian remains in otter faeces, leading to greater accuracy in prey size selection studies.

4.1.4 Comparing diet to prey availability

There are only a small number of studies which have compared otter diet with the availability of prey populations. Erlinge (1967b) compared the results of dietary studies with relevant prey populations estimated using a combination of direct observation, electro-fishing, capture-mark-recapture studies and enquires of local fisherman. Wise *et al.* (1981) compared the diets of both otter and mink with the availability of prey assessed by electro-fishing (for fish species), small mammal trapping and counts of tracks. In both of these studies the conclusions were similar, fish were the main prey and were taken by otters according to availability with some selection for the slower-moving species and often for the smaller fish in the population. Kruuk *et al.* (1993) used electro-fishing to assess populations of salmonids and eels in the River Dee, Aberdeenshire and compared these with the diet and population density of otters in the same areas. It was found that otters seemed to ignore the smallest size classes although this may have been an erroneous conclusion due to the size related differential recovery of salmonid atlas

bones as described earlier. However, in all of these studies no data were provided on the accuracy of the fish population estimates obtained and although in the case of Kruuk *et al.* (1993) it was stated that confidence limits were calculated for population estimates these were not given and appeared to be ignored in their analyses. Fish population estimates obtained using electro-fishing are subject to a number of errors and biases which are dependent on a large number of factors (Bohlin, Hamrin, Heggberget, Rasmussen & Saltveit, 1989). In particular, the efficiency of electro-fishing is heavily affected by the behaviour of different fish species. Shoaling species such as minnows (*Phoxinus phoxinus*) show a strong flight response from the anode and are often heavily stunned in large numbers with a significant proportion of the smallest fish washed away before capture. Therefore, population estimates for species which exhibit shoaling behaviour are usually unreliable. Bottom dwelling species and species which spend time in vegetation, such as eels and stoneloach (*Neomacheilus barbatulus*) also have a low catchability because they tend to be immobilised before they are seen by the operator, or show a strong flight response from the anode which causes them to bury further into the substrate (e.g. stoneloach, pers. obs.), or recover quickly from immobilisation even in close proximity to the anode (e.g. eels, pers. obs.). In many river systems population estimates vary considerably from site to site and unless large numbers of sites are sampled may not be representative of the overall population. Unfortunately, logistic constraints often mean that sample sizes are too small to give accurate population estimates for large areas (Bohlin *et al.*, 1989). These errors must be taken into account when comparing otter diet with prey availability particularly in the light of the number of errors associated with spraint analysis.

It was the aim of the work described in this chapter to assess the diet of otters in the upper Tyne catchment through spraint analysis and to compare this with the availability of the main prey species determined through an electro-fishing survey. The effects of the errors and biases associated with both the spraint analysis and electro-fishing methods are considered and the limitations of the techniques discussed. Geographical variation in the composition of the diet was not assessed in this chapter since Carss & Parkinson (1996) had already shown that spraints collected in an area may not be representative of the fish caught and consumed in that area. This was due to the 24h transit time of food through the digestive system of otters and the large range of otter movements. The

spatial relationship between prey populations, habitat type and the distribution of spraints and spraint sites is, however, discussed in chapter 5.

4. 2 METHODS

4. 2. 1 Spraint analysis

Composition of diet

Otter spraints were collected from a number of sites during each survey period. Not all the spraints encountered were collected for three reasons; (i) some spraints were on rocks in deep and fast flowing water and could not be safely collected; (ii) spraints that were inside the entrance to holts were not collected to avoid disturbance; and (iii) only fresh intact spraints were collected to ensure that the spraint was deposited during the season of collection and that all the material in the spraint was collected. A maximum of five spraints were randomly selected from each 5km stretch which ensured that, in the majority of cases, consecutive spraints were not analysed (all spraints were analysed however from those 5km stretches which contained fewer than five spraints).

Spraints were stored by freezing and were then soaked in a saturated solution of biological washing powder (Biotex) for approximately 48 hours at room temperature before being rinsed through three sieves (1.0, 0.5 and 0.25mm mesh sizes). The washed remains were transferred onto filter paper in petri-dishes and then dried at room temperature. Spraints from the Summer survey were prepared and analysed by an undergraduate, Mark Bailey, under the guidance and supervision of the author.

Using a binocular microscope, at 2-3 times magnification, fish vertebrae and toothed bones were identified to species with the help of a reference collection (prepared by Mark Bailey) and published keys (Maitland, 1972; Webb, 1980 and Conroy, Watt, Webb & Jones, 1993).

The proportions of salmonid vertebrae which were either salmon or trout were calculated from the proportions of atlas bones (first vertebrae) which were used to distinguish between the two species using the methods of Feltham and Marquiss (1989). The proportions of cyprinids which belonged to different species were calculated from the proportions of pharyngeal bones using a published key and reference material to

distinguish between species (Maitland, 1972). Amphibian and mammal skeletal bones were also recorded but because these were low in number and often highly fragmented they were not identified to species. Mammal fur and bird feathers were also recorded as present if encountered. The remains of large invertebrates such as diving beetles (*Dytiscus* spp.) were recorded if present since Carss & Parkinson (1996) showed that these formed a component of the diet even though the captive otters they studied were not directly fed with them. Other smaller invertebrate remains were considered to be from the guts of fish and therefore incidental.

The results of spraint analysis are presented in two ways: - (i) percentage frequency (the proportion of spraints containing a prey type) for all prey groups and; (ii) relative frequency (the number of occurrences of a particular prey item as a percentage of all recorded items) for fish prey only. Ninety-five percent confidence intervals (CI) were calculated from binomial sampling as used by Jenkins, *et al.*, 1979; Jenkins and Harper, 1980; Carss & Parkinson, 1996 (Equation 4.1)

$$CI(95\%) = p \pm z\sqrt{(p(1-p) / n)} \qquad (4.1)$$

where p is the percentage occurrence or relative frequency (as a proportion) , z is equal to 1.96 and n the number of spraints or prey items.

Percentage frequency and relative frequency were calculated for each seasonal survey and for the overall sample.

Size of fish in the diet

Salmonids

The sizes of salmonid prey were calculated in two ways. First, the length of all caudal and thoracic vertebrae encountered were measured to the nearest 0.1mm under a binocular microscope fitted with an eyepiece graticule. These measurements were then converted to snout-fork length estimates using the following equations for thoracic and caudal vertebrae adapted from Wise (1980)

$$FL = 72VL(caudal) + 12.1 \quad (4.2)$$

$$FL = 75.1VL(thoracic) + 19.5 \quad (4.3)$$

where FL was the snout to fork length and VL was the vertebral length in millimetres.

The second method used atlas bones to distinguish between salmon and trout and the width of this bone measured under a binocular microscope as before. This measurement was then converted to snout to fork length using equation 4.4 (from Feltham & Marquiss, 1989)

$$FL = 60.5VW\ (atlas) - 8.95 \quad (4.4)$$

where FL was the snout to fork length and VW was the atlas width in millimetres.

Eel

The sizes of eels in the diet were determined as for salmonids, by measuring under a microscope the length of thoracic vertebrae which Wise (1980) found to vary least in length in relation to eel body length. Carss and Elston (1996) showed that this variation increased with increasing body length and produced an equation relating vertebral length to fish length (equation 4.5) which took this into account. This equation was used in this study to estimate eel snout to fork length.

$$FL = 113T_i + 9.08 \quad (4.5)$$

where FL was the snout to fork length and T_i was the thoracic vertebral length in millimetres.

Cyprinids

All of the pharyngeal bones encountered in this study that were identifiable were from minnows (see section 4.2). Therefore, it was assumed that all cyprinids in the diet were

minnow. The sizes of minnow in the diet were determined from pharyngeal bones using 'gape' measurements as described by Mann and Beaumont (1980) which were then converted to snout to fork length using their regression equation (equation 4.6).

$$FL = 8.57 + 16.54(GAPE) \quad (4.6)$$

where FL was the snout to fork length and GAPE was the gape of the pharyngeal bone in millimetres.

Stoneloach

The sizes of stoneloach in the diet were estimated from measurement of caudal and thoracic vertebrae as for salmonids using equations from Wise (1978) (equations 4.7 and 4.8).

$$FL = 59.3VL \text{ (caudal)} + 5.1 \quad (4.7)$$

$$FL = 48.9VL \text{ (thoracic)} + 5.2 \quad (4.8)$$

where FL was the snout to fork length and VL was the vertebral length in millimetres.

Other fish species

Bullhead (*Cottis gobio*) and lamprey (*Lampetra* spp.) remains were not found in otter spraints from the Tyne catchment and stickleback (*Gasterosteus aculeatus*) formed only a minor component of the diet. Therefore no attempt was made to determine the sizes of these species from their remains.

Each prey item measured was then assigned to a particular size class for each species and the proportions for each size class calculated by dividing the number of prey items in each size class by the total number of prey items measured for each species.

Carss and Elston (1996) demonstrated that the atlas bones of larger salmonids were more likely to be recovered in spraints than those from smaller ones and that the "recovery probability" for any fish length was described by equation 4.9.

$$\text{recovery probability} = \exp[k_i] / (1 + \exp[k_i]) \qquad (4.9)$$

where $k_i = 0.40 + 0.014 (L_i - 120)$ where L_i is the estimated snout to fork length in millimetres.

They also demonstrated that the proportion of measurable eel thoracic vertebrae found in spraints decreased with increasing fish length and that the "recovery probability" for any fish size was also described by equation 4.9 except that in this case k_i was derived from equation 4.10.

$$k_i = 0.657 - 4.63 \times 10^{-3} L_i \qquad (4.10)$$

Therefore, for salmonid lengths derived from atlas bones and eel lengths derived from thoracic vertebrae the number of prey items in each size class was divided by the "recovery probability". This produced an estimate of the frequency which takes into account these size related differential recovery rates. These values were then converted to proportions as before.

The "recovery probabilities" for other species were unknown and therefore the results obtained for minnow and stoneloach should be interpreted with some caution since it was possible that the bones recovered from these species also exhibited size-related differential recovery rates.

4.2.2 Electro-fishing

Prey availability was determined from the results of an electro-fishing survey conducted by the author and two assistants from Durham University (Mark Bailey and Dr. Mick Hanley) between July and September 1995 at 97 sites throughout the catchment. Training in electro-fishing was provided by Dr. Martyn Lucas of Durham University prior to the Tyne survey. Sites were selected within each 5km stretch and were chosen

on the basis of accessibility and landowner permission. This meant that for most 5km stretches two or three sites were selected (see Figure 4.2.1) for electro-fishing. Only one site was accessible for electro-fishing in one 5km stretch and in another stretch permission to fish was not given. It would have been preferable for all sites to have been chosen at random. However, this was not practical since the electro-fishing method required the use of heavy and bulky equipment which meant that reasonable access to the sites was required. The sites were, however, chosen from maps prior to the survey so the habitat and physical characteristics of the river were unknown until the site was fished.

At each site a $100m^2$ area of river or stream was measured as accurately as possible using a tape measure to assess length and determining the width by averaging the widths sampled at three points along the length. The downstream and upstream ends were then delimited by 9mm mesh block nets thus restricting fish movements to the fishing area. Where the river or stream was less than 10m wide the entire width of the stream was enclosed. For those sites that were wider than this a 10m width was delimited. Fishing was carried out in an upstream direction using a single anode powered by a 2kW generator at less than 300 volts depending on the conductivity of the water. Previous to the main programme practice sessions had shown that minnow mortality was high when using pulsed d.c., so non-pulsed d.c. was used throughout the survey. Fish that were attracted or immobilised by the anode were caught in hand nets and transferred to holding buckets on the bank. Most sites were fished three times with a 30 minute break between fishings, although at some sites with low numbers of fish and almost complete depletion after the first fishing only two fishings were carried out.

All fish were anaesthetised using a weak solution of buffered tricaine methane sulphonate (MS-222), identified to species and then measured (to the nearest millimetre) from tail fork to snout. Fish were then placed in a recovery bucket before being returned to the river after the completed series of fishings. When large numbers of fish were caught and temperatures were high, fish were returned to the river downstream of the fishing site after a 20-30 minute recovery period. Population estimates were calculated for each site using the methods of Bohlin *et al.* (1989). For three removals, with populations of greater than 50 fish and a first catch of greater than 25, the population estimate (y) was determined using equation 4.11 where $A = 2c_1 + c_2$ and $T = c_1 + c_2 + c_3$ (c_1, c_2 and c_3

being the total number of fish in the first, second and third removals respectively). The variance of this estimate was calculated from equation 4.12 where p is the catchability and was calculated from equation 4.13 and q is equal to 1 - p. The Standard Errors (SE(y)) are the square root of equation 4.12 enabling 95% confidence limits to be calculated from equation 4.14.

$$y = \frac{6A^2 - 3AT - T^2 + T\sqrt{T^2 + 6AT - 3A^2}}{18(A - T)} \tag{4.11}$$

$$V(y) = \frac{y(1 - q^3)q^3}{(1 - q^3)^2 - (3p)^2 q^2} \tag{4.12}$$

$$p = \frac{3A - T - \sqrt{T^2 + 6AT - 3A^2}}{2A} \tag{4.13}$$

$$95\%CL = y \pm 2SE(y) \tag{4.14}$$

For populations smaller than 50 or with a first catch of less than 25 or where less than three fishings were carried out an approximately known catchability was calculated after Bohlin *et al.* (1989). In this case y and p were calculated from the pooled results of all sites where three removals had been carried out using equations 4.11 and 4.13 respectively. The resultant p (and therefore q) then had good precision and was used in equation 4.15 to determine y. The precision in this case was partly determined by the precision of the p estimate from the pooled result (Bohlin *et al.*, 1989) with the sampling variance (V(y)) being calculated from equation 4.16 where the variance of p (i.e. V(p)) was calculated from equation 4.17 and k was the number of removals. Standard Errors and 95% confidence limits calculated as before.

$$y = \frac{T}{(1 - q^k)} \tag{4.15}$$

$$V(y) = \frac{yq^k}{1 - q^k} + V(p)\left(\frac{ykq^{k-1}}{1 - q^k}\right)^2 \tag{4.16}$$

$$V(p) = \frac{(qp)^2(1-q^k)}{y[q(1-q^k)^2 - (kp)^2 q^k]} \qquad (4.17)$$

Bohlin *et al.* (1989) stated that the Standard Error estimate was doubtful if the population estimate was smaller than about 200 for the 2-catch method and about 50 for the 3-catch method. Therefore variances were not calculated for any sites where this occurred which meant that no estimate of the sampling precision could be obtained for these sites. Population estimates, variances and 95% confidence limits were calculated (where possible) for each species encountered at each site using a combination of Microsoft Excel spreadsheets and SPSS for Windows statistical software.

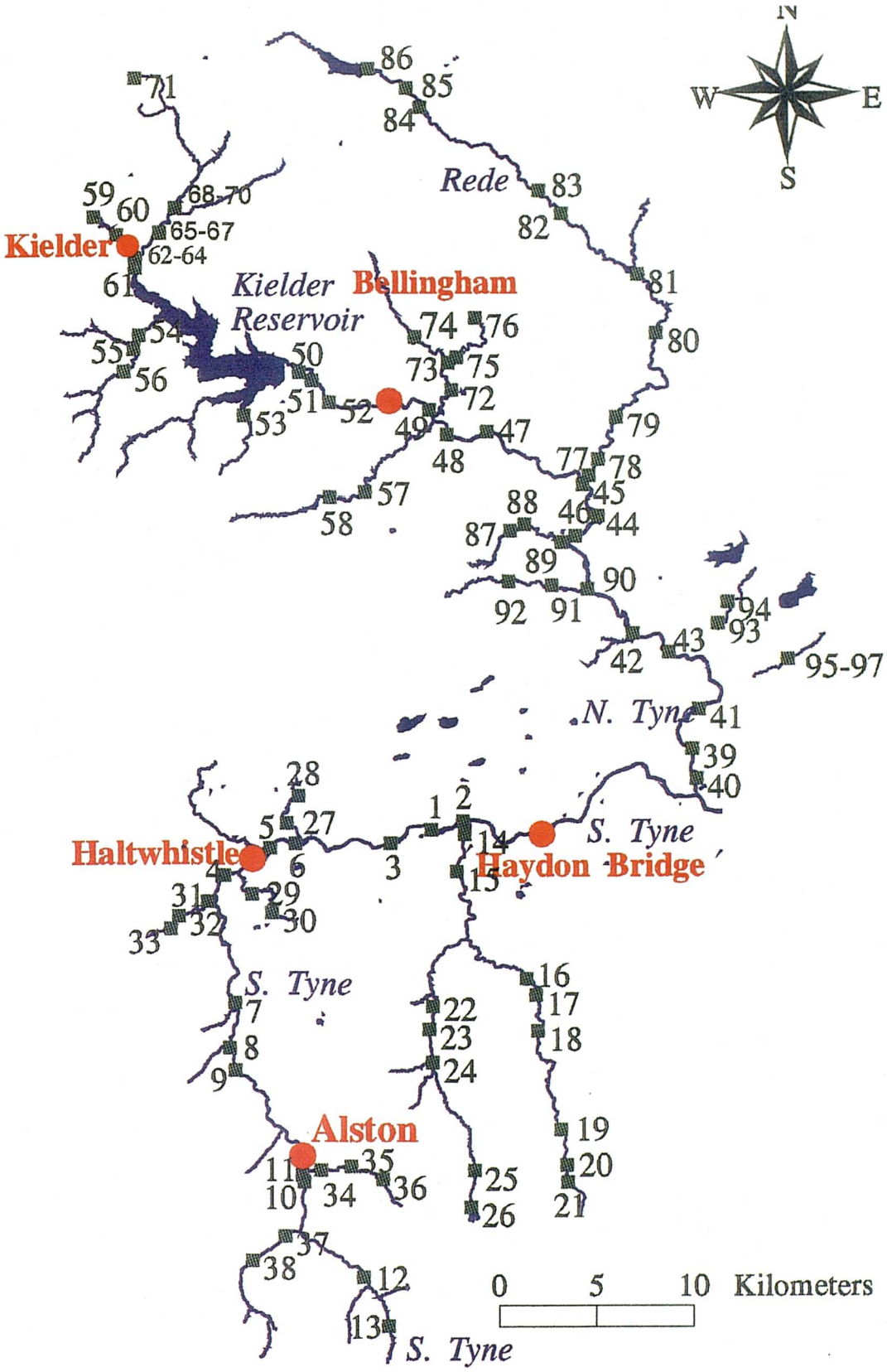


Figure 4.2.1 Map showing the locations of sites fished during an electro-fishing survey to determine fish populations in the upper Tyne catchment in the summer of 1995.

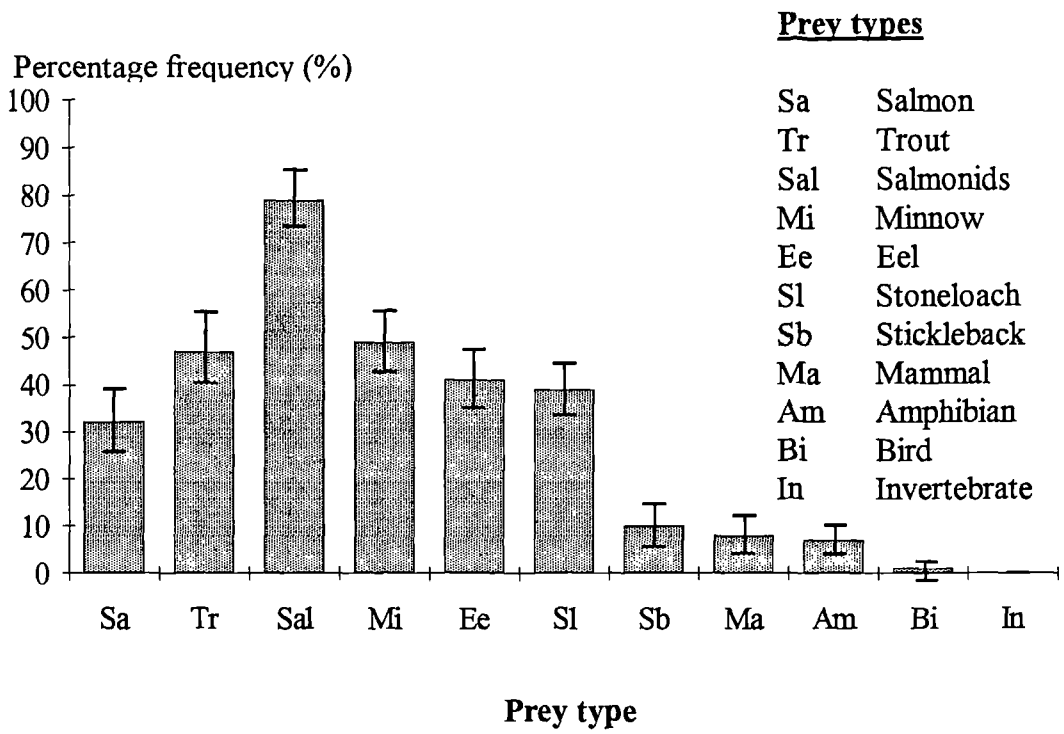
4.3 RESULTS

4.3.1 Spraint analysis

Composition of the diet

Table VI.I in Appendix VI gives the numbers of spraints and the percentage frequency and relative frequency of prey items found in otter spraints collected from the upper Tyne catchment for each of the four seasonal surveys and for the overall sample. All of the identifiable cyprinid pharyngeal bones (n = 152) found in the spraints were from minnows. No large invertebrate remains were found. Figure 4.3.1 shows the percentage frequency (a) and relative frequency (b) of prey items found in the spraints for the overall sample together with 95% confidence intervals (shown as bars). These confidence intervals were wide for the percentage frequency data but the predominance of salmonids in the diet (79% of spraints containing salmonid remains, 50% of all occurrences) was clearly shown. All other species formed a much lower component than salmonids with stickleback, mammals and amphibians combined forming a minor component of the diet, 0-12% of spraints (Figure 4.3.1a). The width of the confidence intervals made it impossible to determine differences in the occurrence of other fish species except that salmon formed a lower component (25-39% of spraints) of the diet than trout (40-54% of spraints), minnow (42-56% of spraints) eel (34-48% of spraints) and stoneloach (32-46% of spraints), although the confidence limits overlap between salmon and these two latter species. The relative frequency data (Figure 5.3.1b) confirmed these findings with salmonids forming the largest fish component of the diet (49-51% of all occurrences) of which trout was the more important (29-31% of all occurrences). Minnow formed a higher component of the diet than salmon (23-25% compared with 19-21% of occurrences) although in this case salmon formed a higher component than all the remaining species.

(a) Percentage frequency



(b) Relative frequency

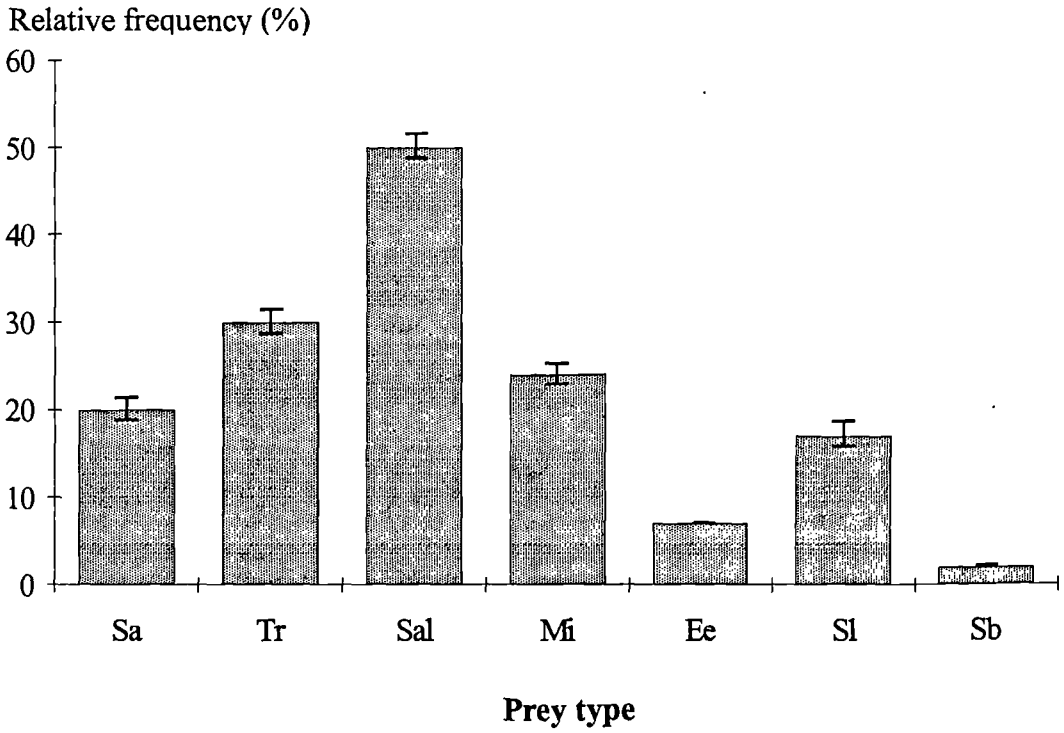


Figure 4.3.1 Percentage frequency (a) and Relative frequency (b) of the main prey items found in otter spraints collected from the upper Tyne catchment between 1993 and 1994. Vertical bars represent 95% Confidence Intervals.

These findings may, however, mask seasonal differences in the composition of the diet of otters in the upper Tyne catchment. Figure 4.3.2. therefore, presents histograms of percentage frequency (a) and relative frequency (b) of prey items found in spraints for each season. Interpretation of these figures should be treated with some caution due to the wide confidence intervals resulting from small sample sizes but a number of broad conclusions can be drawn. The percentage frequency histograms (Figure 4.3.2a) show that salmonids were the most important component of the diet in the Spring (70-88% of spraints), Autumn (72-98% of spraints) and Winter (85-100% of spraints). In the Spring and Autumn samples all other prey types apart from stickleback, mammals and amphibians (which formed only a minor component of the diet) assumed equal importance in the diet. In the Winter sample minnows were the only other major component of the diet (47-77% of spraints). In the Summer sample, however, salmonids and eels were equally important (58-72% of spraints and 49-77% of spraints respectively). These two species appeared to be more important in the Summer diet than minnow (27-55% of spraints) and stoneloach (31-59% of spraints) although this conclusion should be treated with some caution since there was some overlap of confidence intervals. In all seasons trout appeared to be a more important component of the diet than salmon confirming the results observed for the overall sample. However, there was considerable overlap of the 95% confidence intervals for these two species again making this conclusion tentative.

Histograms of relative frequencies for each fish prey (Figure 4.3.2b) confirmed the importance of salmonids in all seasons (29-65% of occurrences) although minnows formed the highest component of the diet in the Autumn sample (49-55% of occurrences) compared to salmonids (26-32% of occurrences).

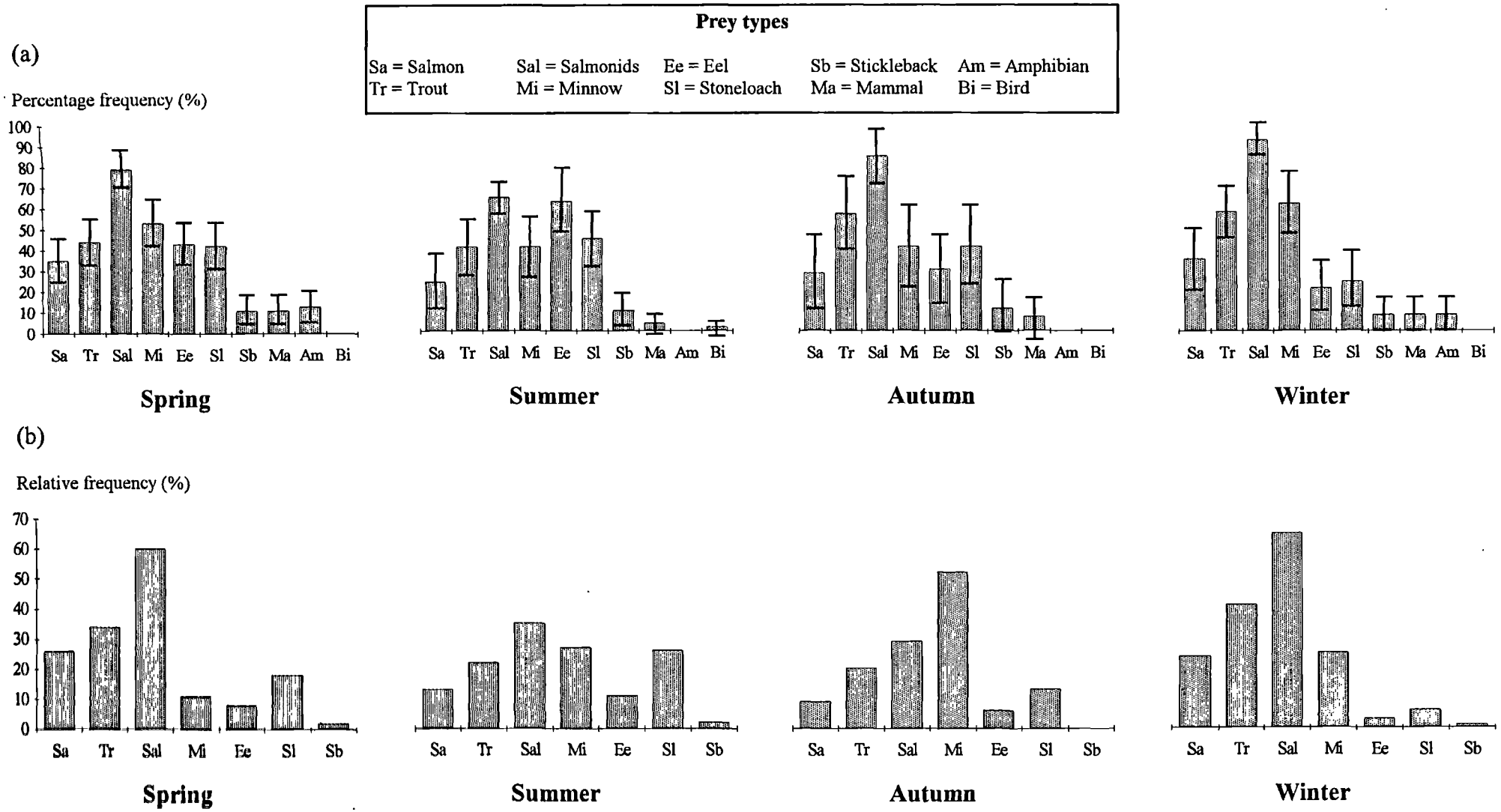


Figure 4.3.2 Percentage frequencies (a) and relative frequencies (b) for the main prey types found in otter spraints collected during four seasonal surveys of the upper Tyne catchment between 1993 and 1994. Vertical lines represent 95% Confidence Intervals. These were too narrow to be represented graphically for relative frequencies.

The width of the confidence intervals made statistical comparisons of each species between seasons impossible but Figure 4.3.3a shows that there was a general pattern of low Summer and high Winter percentage frequencies of salmon and trout in the diet and low percentage frequencies of stoneloach in the Winter. When total salmonids were considered this pattern of low Summer and high Winter percentage frequency was even clearer. Conversely the percentage frequency of eels in the diet was at its highest in the Summer and at its lowest in the Winter. There was little difference in the percentage frequency of stickleback between seasons and the occurrence of mammal, amphibian and bird remains was too low to show any meaningful seasonal differences. These general seasonal patterns were confirmed by the histograms of relative frequency for each species (Figure 4.3.3b) where salmonids were at their lowest in the Summer and Autumn samples and at their highest in the Spring and Winter samples. The relative frequency of eels was highest in the Summer sample and lowest in the Winter sample while the relative frequency of minnows was lowest in the Spring sample and highest in the Autumn sample. The relative frequency of stoneloach was highest in the Summer sample falling to virtually zero in the Winter sample while the relative frequency of stickleback showed little seasonal differences.

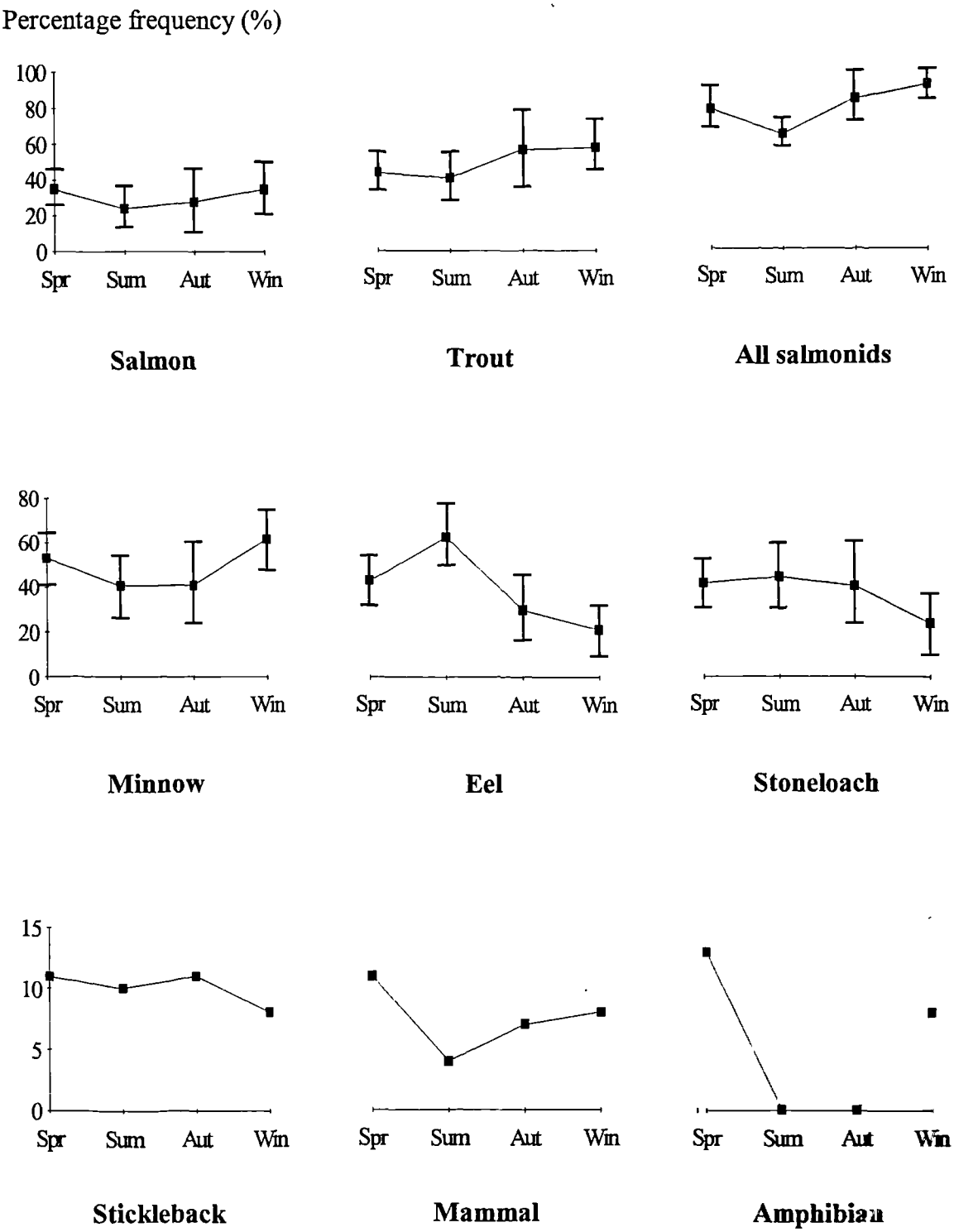


Figure 4.3.3a Seasonal differences in the percentage frequency of the main prey items found in otter spraints collected from the upper Tyne catchment between 1993 and 1994. Vertical bars represent 95% Confidence Interval. These were too narrow to be represented graphically for stickleback, mammal and amphibian.

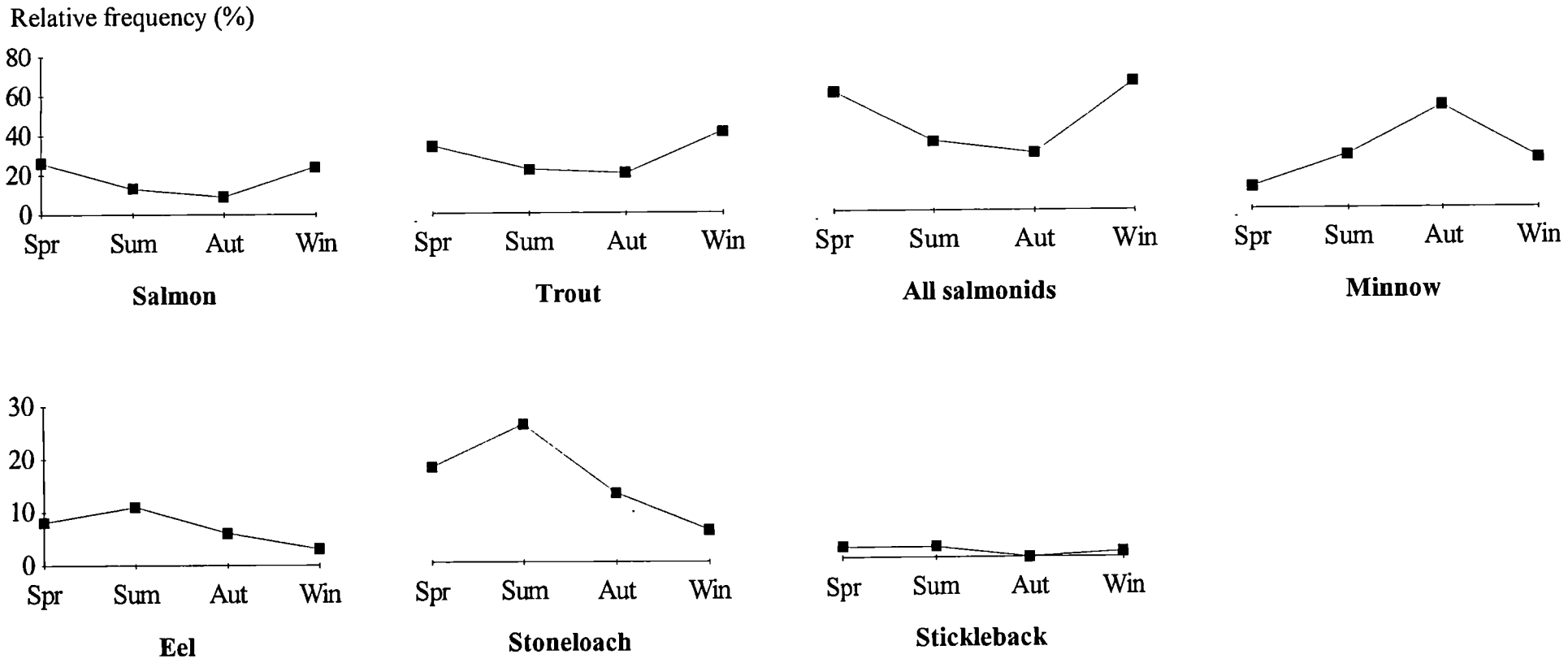


Figure 4.3.3b Seasonal differences in the relative frequencies of the main prey items found in otter spraints collected from the upper Tyne catchment between 1993 and 1994. 95% Confidence Intervals were too narrow to be represented graphically.

Size of fish in the diet

Salmonids

Table 4.3.1 shows the size classes for each of the six main prey types found in otter spraints collected from the upper Tyne catchment.

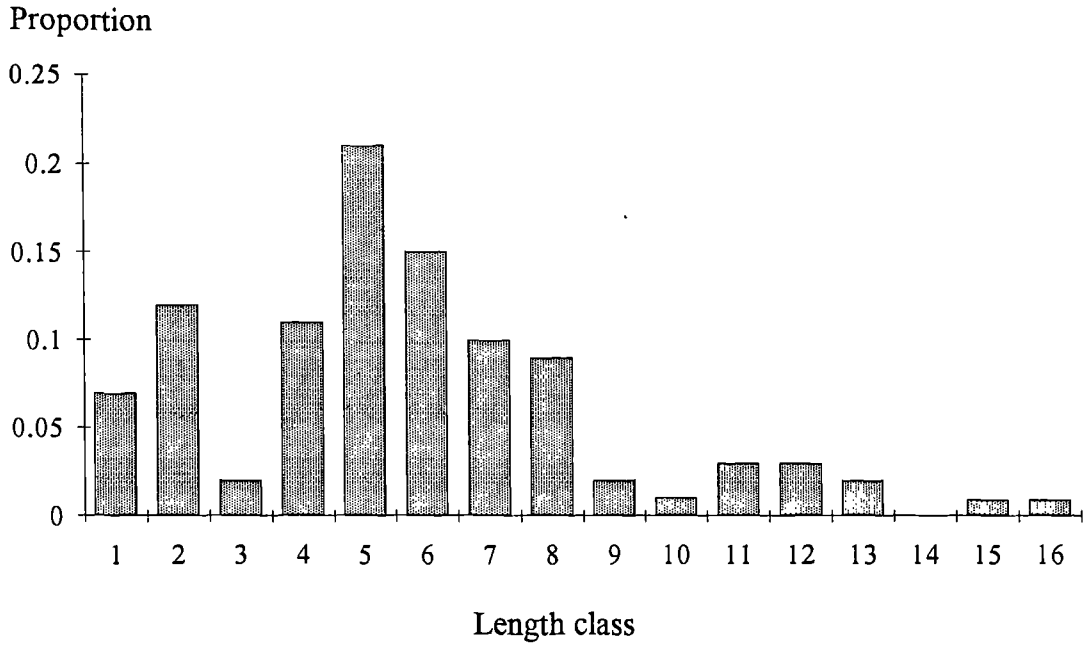
Table VI.II in Appendix VI gives the frequencies and the proportions of fish in each length class estimated from the widths of salmonid atlas (first vertebra) bones found in spraints collected during the four seasonal surveys of the upper Tyne catchment between 1993 and 1994. Corrected frequencies and proportions which take into account size related differential recovery of atlas bones are also provided.

The distribution of salmonid fish lengths estimated from atlas bones and corrected for size-related differential recovery was polymodal (Figure 4.3.4a) with modes at size class 2 (>30≤40mm), size class 5 (>60≤70mm) and between size classes 11 and 12 (>120≤140mm). The largest proportion of fish were in the size class 4-8 range (>50≤90mm). There was a higher proportion of salmon than trout in the smaller size classes 2 and 3 (>30≤50mm) and a higher proportion of trout than salmon in the larger size classes (>130mm) (Figure 4.3.4b). However, these differences were not statistically significant (χ^2 = 10.9, 6df, NS, see Table 4.3.2). The low number of atlas bones recovered (n = 66) provided sample sizes too small to allow seasonal comparisons of prey size in the otter's diet in the upper Tyne catchment. It would be desirable therefore to be able to use the fish length estimates derived from caudal and thoracic vertebrae which were more numerous in the spraints (n = 2282 and n = 2145 respectively). However, as Carss & Elston (1996) showed, these bones provided variable estimates of actual fish length and as Table 4.3.3 shows, thoracic vertebrae produced estimates of the salmonid length distribution in the diet of otters in the upper Tyne catchment that differed significantly from estimates from caudal vertebrae (χ^2 = 468, 14 df, $p < 0.001$). If, however, it is assumed that the width of atlas bones provided a reasonable approximation of the distribution of actual fish lengths then the vertebrae (thoracic or caudal) which most closely matched this distribution should also provide a reasonable approximation of actual fish lengths. Table 4.3.4. shows that there were highly significant differences in fish length distributions between those derived from atlas bone

Table 4.3.1 Size classes for the main prey types in otter spraints collected during four surveys of the upper Tyne catchment between March 1993 and November 1994.

Class	length (mm)			
	salmon	eel	stoneloach	minnow
1	≤30	≤150	≤30	>20≤25
2	>30≤40	>150≤200	>30≤40	>25≤30
3	>40≤50	>200≤250	>40≤50	>30≤35
4	>50≤60	>250≤300	>50≤60	>35≤40
5	>60≤70	>300≤350	>60≤70	>40≤45
6	>70≤80	>350≤400	>70≤80	>45≤50
7	>80≤90	>400≤450	>80≤90	>50≤55
8	>90≤100	>450≤500	>90≤100	>55≤60
9	>100≤110	>500≤550	>100≤110	>60≤65
10	>110≤120	>550≤600	>110	>65≤70
11	>120≤130	>600		>70≤75
12	>130≤140			>75≤80
13	>140≤150			>80≤85
14	>150≤160			>80
15	>160≤170			
16	>170			

(a) All salmonids



(b) Salmon and Trout

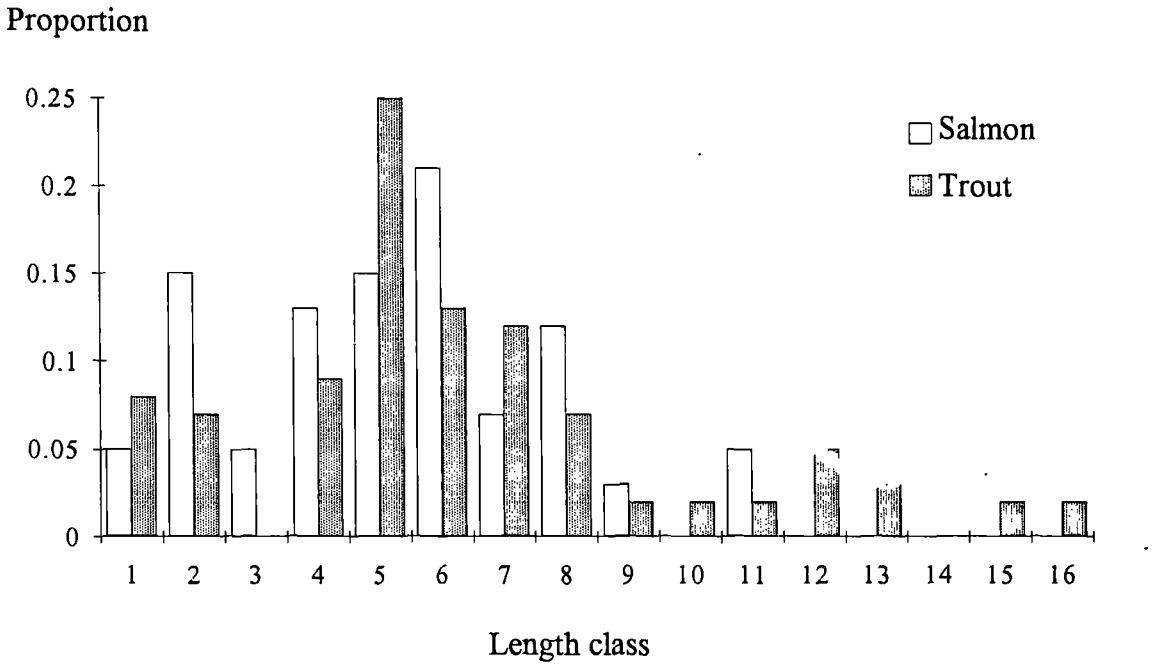


Figure 4.3.4 Distribution of all salmonid (a) and salmon and trout (b) lengths in the diet of otters estimated from atlas bones (n = 66, 27 and 39 respectively) found in spraints collected during four seasonal surveys of the upper Tyne catchment between 1993 and 1994. Frequencies in each length class were corrected for size-related differential recovery of atlas bones after Carss & Elston (1996).

Table 4.3.2 Comparison of the frequencies of salmon and trout in each size class estimated from atlas bones found in otter spraints collected during four seasonal surveys of the upper Tyne catchment between 1993 and 1994. The frequencies of fish in each size class were corrected for size-related differential recovery of atlas bones (Carss, 1996). Some of the original 16 size classes were combined to ensure that all expected frequencies in the χ^2 analysis were greater than 5.

Length class (mm)	Frequency		
	Salmon	Trout	Total
≤40	12.9	13.0	25.9
>40≤60	11.0	7.9	18.9
>60≤70	9.7	21.8	31.5
>70≤80	13.5	11.2	24.7
>80≤90	4.3	10.7	15
>90≤100	7.7	5.9	13.6
>100	5.1	15.4	20.5
Total	64.2	85.9	150.1

$\chi^2 = 10.9$, 6df, NS.

Table 4.3.3 Comparison of the frequency distributions of salmonids in each size class estimated from caudal and thoracic vertebrae found in otter spraints collected during four seasonal surveys of the upper Tyne catchment between 1993 and 1994. Some of the original 16 size classes were combined to ensure that all expected frequencies in the χ^2 analysis were greater than 5.

Length class (mm)	Frequency		
	Caudal	Thoracic	Total
≤50	315	148	463
>50≤60	256	275	531
>60≤70	688	487	1175
>70≤80	216	754	970
>80≤90	147	155	302
>90≤100	171	162	333
>100≤110	72	128	200
>110≤120	61	61	122
>120≤130	108	37	145
>130≤140	34	32.	66
>140≤150	40	7	47
>150≤160	16	13	29
>160≤170	7	11	18
>170≤180	7	4	11
>180	7	8	15
Total	2145	2282	4427

$\chi^2 = 468$, 14df $p < 0.001$.

Table 4.3.4 Comparison of the frequency distributions of salmonid fish lengths estimated from atlas bones and caudal (a) and thoracic (b) vertebrae found in otter spraints collected during four seasonal surveys of the upper Tyne catchment between 1993 and 1994 Some of the original 16 length classes have been combined to ensure that all expected frequencies in the χ^2 analysis were greater than 5.

(a) Atlas versus caudal

Length class (mm)	Frequency		
	Atlas	Caudal	Total
≤50	28.8	315	343.8
>50≤60	16.0	256	272
>60≤70	31.5	688	719.5
>70≤80	24.7	216	240.7
>80≤90	15	147	162
>90≤100	13.6	171	184.6
>100≤120	5.3	133	138.3
>120≤130	4.9	108	112.9
>130	10.3	111	121.3
Total	150.1	2145	2376.8

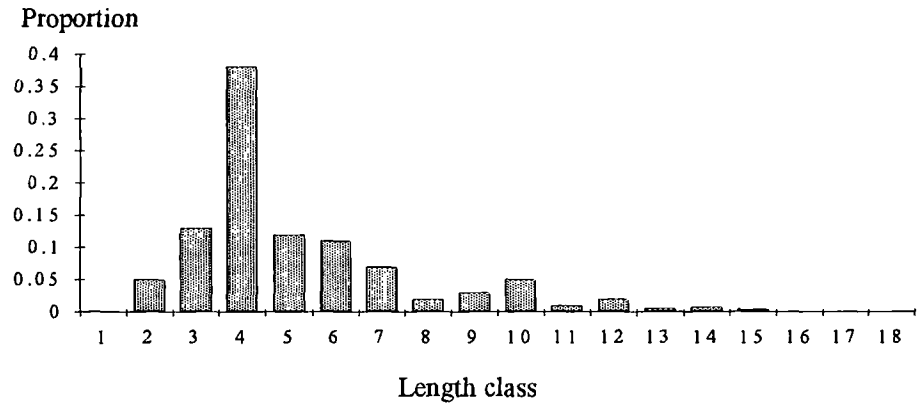
$\chi^2 = 21.9$, 8df, $p < 0.01$

(b) Atlas versus thoracic

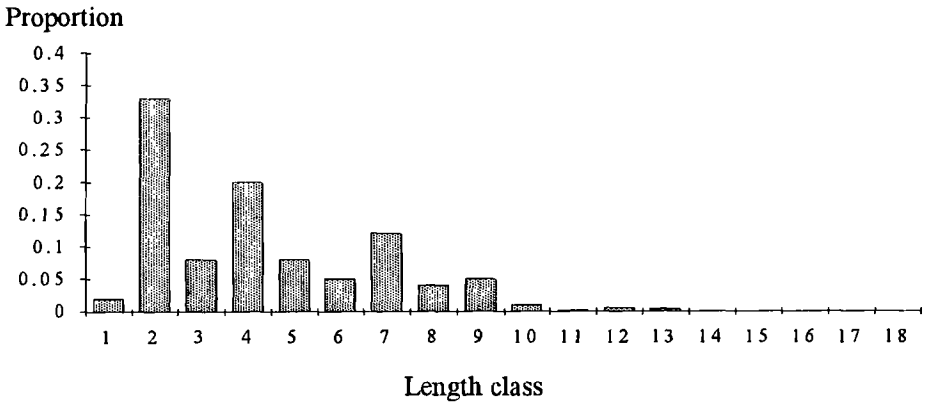
Length class (mm)	Frequency		
	Atlas	Thoracic	Total
≤50	28.8	148	176.8
>50≤60	16.0	275	291
>60≤70	31.5	487	518.5
>70≤80	24.7	754	778.7
>80≤90	15	155	170
>90≤100	13.6	162	175.6
>100≤120	5.3	189	194.3
>120	15.2	112	127.2
Total	150.1	2282	2432.1

$\chi^2 = 57.7$, 7df $p < 0.001$

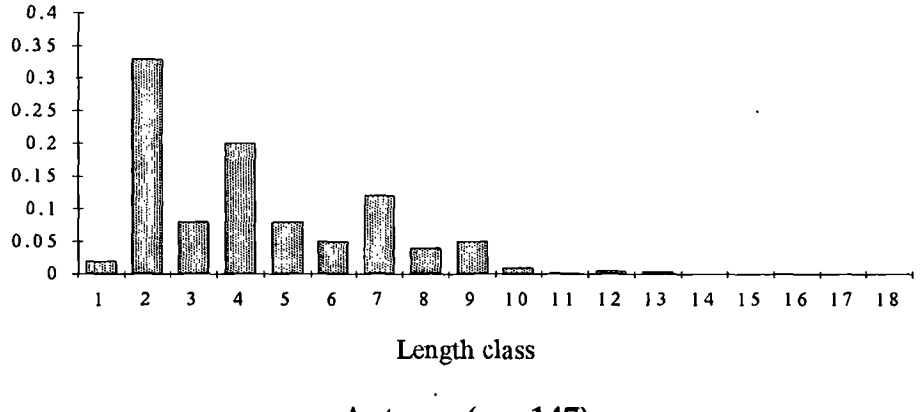
and both caudal vertebra ($\chi^2 = 21.9$, 8df $p < 0.01$, Table 4.3.4a) and thoracic vertebra ($\chi^2 = 57.7$, 7df $p < 0.01$, Table 4.3.4b). This suggested that the lengths of neither caudal nor thoracic bones were good estimators of actual fish length distributions. However, if it is assumed that the errors in estimating fish lengths are the same in each season then at least relative seasonal changes in the lengths of salmonid prey can be assessed. Table VI.III in Appendix VI gives the frequencies and proportions of salmonids in each size class for both caudal and thoracic vertebrae in each season. Figure 4.3.5 shows the fish length distribution in each season derived from thoracic (a) and caudal (b) vertebrae. For caudal vertebrae there was a peak in all seasons at size class 4 (>60≤70mm). In the Summer and Autumn samples however, there was a larger peak at size class 2 (>40≤50) and in the Autumn and Winter samples there were small peaks at size class 8 (>100≤110mm) and size class 10 (>120≤130). For thoracic vertebrae there was a peak at size class 5 (>70≤80mm) in all seasons. In addition, in the Summer sample there was also a peak at size class 2 (>40≤50) although there were no obvious peaks in the larger size classes in any season.



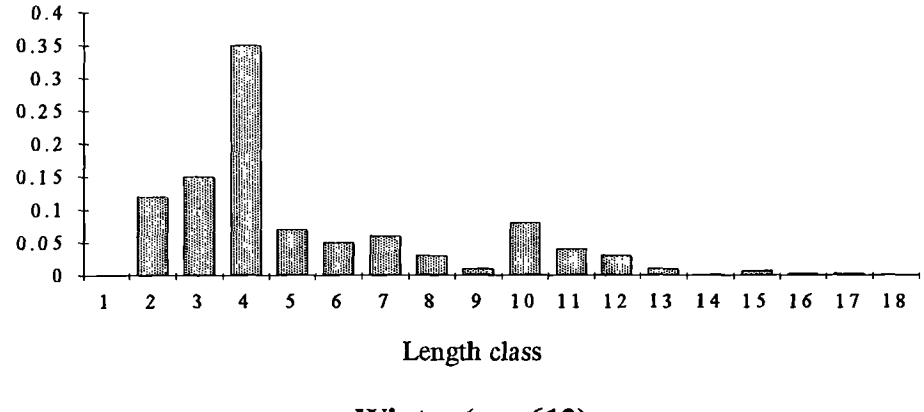
Spring (n = 823)



Summer (n = 559)

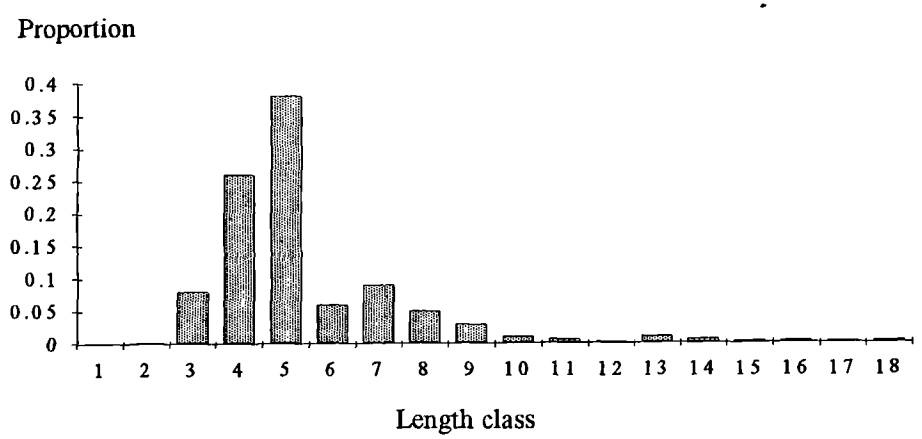


Autumn (n = 147)

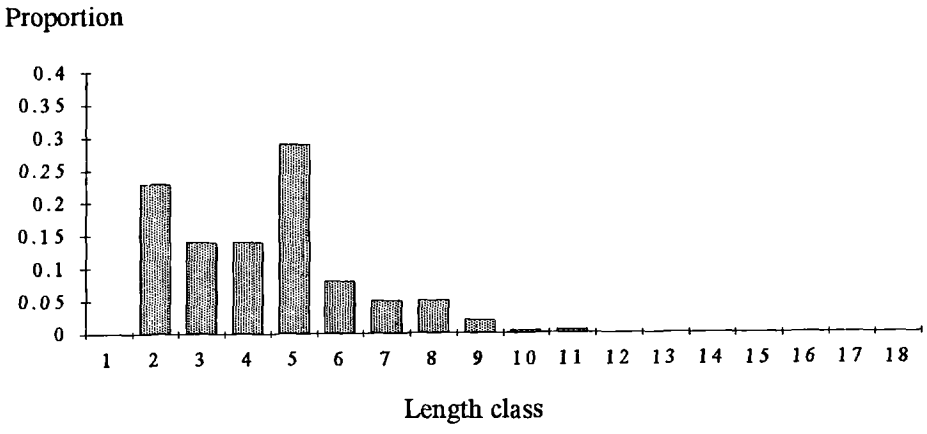


Winter (n = 613)

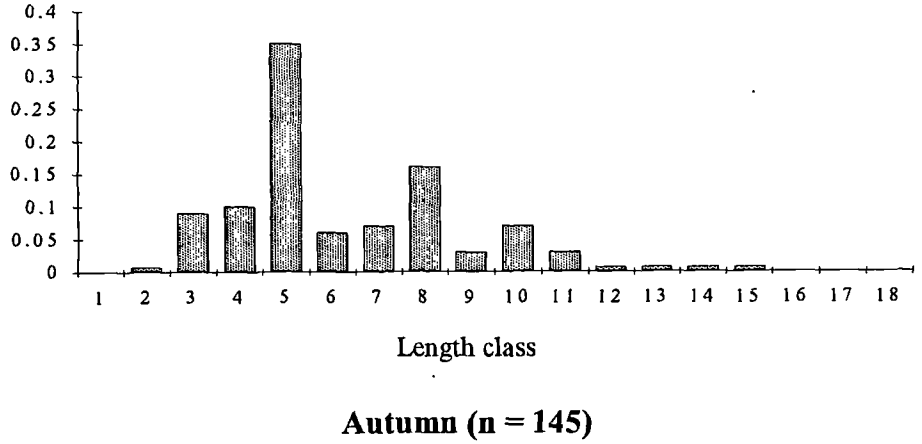
Figure 4.3.5a Distribution of salmonid fish lengths in the diet of otters estimated from the lengths of caudal vertebrae found in spraints collected during four seasonal surveys of the upper Tyne catchment between 1993 and 1994.



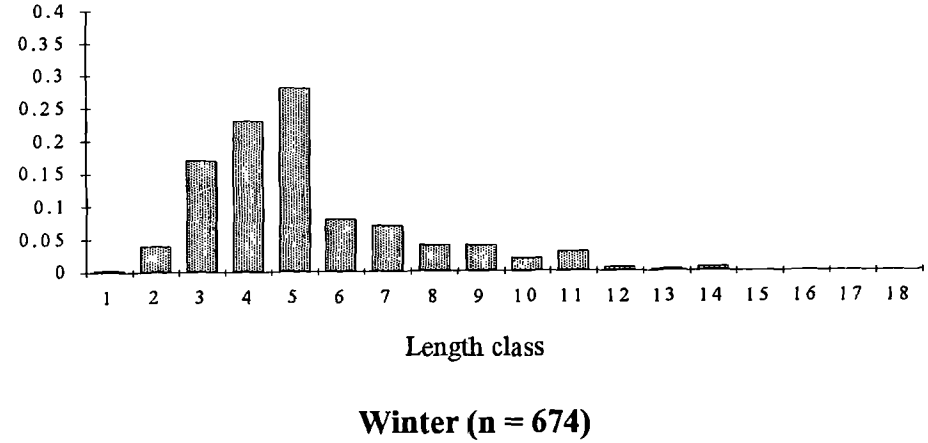
Spring (n = 950)



Summer (n = 510)



Autumn (n = 145)



Winter (n = 674)

Figure 4.3.5b Distribution of salmonid fish lengths in the diet of otters estimated from the lengths of thoracic vertebrae found in spraints collected during four seasonal surveys of the upper Tyne catchment between 1993 and 1994.

Table VI.IV in Appendix VI gives the frequencies and proportions of eels in each length class estimated from the lengths of thoracic vertebrae found in spraints collected during the four seasonal surveys. Corrected frequencies and proportions which take account of the size-related differential recovery of eel thoracic vertebrae are also provided. Figure 4.3.6 shows that the majority of eels in the diet were between size class 3 and size class 7 (>200≤450mm) with smaller peaks at size class 1 (<150mm) and size class 11 (>600mm).

However, as with salmonids, it was possible that this pooled sample masked seasonal differences in the sizes of eels in the diet. Unfortunately full seasonal comparisons could not be conducted due to the small number of vertebrae in the Spring and Winter samples. Therefore, to compare seasonal differences in the eel length distributions Spring, Winter and Autumn samples were combined and then compared with the Summer sample (Table 4.3.5). It was shown that the Summer length distribution differed significantly from the distribution in other seasons ($\chi^2 = 84$, $p<0.001$ at 7 degrees of freedom) with more eels in size class 4 (>250≤300mm) in the summer than in the other seasons.

Table 4.3.5 Comparison of seasonal differences in the distributions of eel lengths in the diet of otters estimated from the lengths of thoracic vertebrae found in spraints collected during four surveys of the upper Tyne catchment 1993-1994.

Length class (mm)	Summer		Other	
	f	p	f	p
≤150	1.9	0.007	9.6	0.04
>150≤200	2.1	0.008	2.2	0.01
>200≤250	53.1	0.20	24.3	0.11
>250≤300	65.8	0.24	17.4	0.08
>300≤350	48.5	0.18	79.7	0.36
>350≤400	15.2	0.06	36	0.16
>400≤450	19.8	0.07	24	0.04
>450≤500	5.2	0.02	27	0.12
>500	10.3	0.04	0	0
n	71 vertebrae		64 vertebrae	

$\chi^2 = 84$, 7df, $p<0.001$

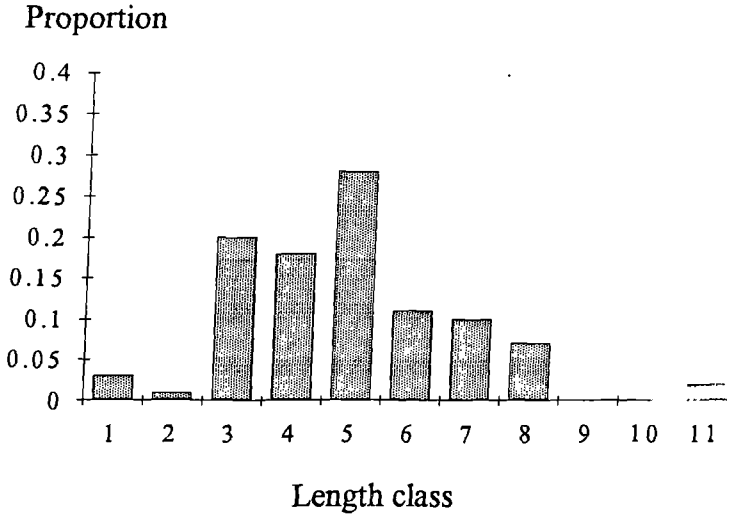


Figure 4.3.6 Distribution of eel lengths in the diet of otters calculated from the lengths of thoracic vertebrae (n = 135) found in spraints collected from the upper Tyne catchment between 1993 and 1994. All length frequency classes were corrected for size related differential recovery of thoracic vertebrae after Carss (1996).

Minnow

Table VI.V in Appendix VI gives the frequencies and proportions of minnows in each size class in each season and for the overall sample for minnow fish lengths estimated from the 'gape' measurement of pharyngeal bones. Figure 4.3.7e shows that overall there were two peaks in the minnow fish length distribution with the highest peak occurring at size class 6 (45≤50mm) and a secondary peak at size class 3 (<30≤35mm). The minnow fish length distributions were found to differ significantly between seasons (Friedman 2-way ANOVA = 9.72, 3df, $p < 0.05$). The procedure of multiple comparisons (Coshall, 1989) was used to determine which seasons differed significantly in fish length distributions. Table 4.3.6 shows that the principal reason for rejecting the null hypothesis of no difference in fish length distribution between seasons was due to the significant difference in length distributions between Autumn and all other seasons. This result is confirmed by Figure 4.3.7a-d which shows that in all seasons the majority of fish were between size classes 5 and 8 (>40≤60mm) but that in the Autumn sample there was a secondary peak at size class 3 (>30≤35mm) which did not occur in any other season.

Table 4.3.6 Friedman multiple comparisons test of the absolute differences, $|R_u - R_v|$, between seasons in the lengths of minnows estimated from pharyngeal bones found in otter spraints collected during four seasonal surveys of the upper Tyne catchment between 1993 and 1994.

	u			
v	1 (Spring)	2 (Summer)	3 (Autumn)	4 (Winter)
1 (Spring)	-			
2 (Summer)	16	-		
3 (Autumn)	48**	32**	-	
4 (Winter)	8	8	40**	-

** Significant at $p < 0.01$

Table VI.VI in Appendix VI gives the frequencies and proportions of stoneloach in each size class for the overall sample of stoneloach as estimated from the lengths of both caudal and thoracic vertebrae. It was found that the length distribution estimated from caudal vertebrae differed significantly from that estimated from thoracic vertebrae (χ^2 = 40.0, 9df $p < 0.01$). This showed that one or both of the two vertebrae types was not a good estimator of actual fish lengths. Unfortunately without feeding trials of the kind conducted on captive otters by Carss & Elston (1996) it was impossible to determine which vertebra type provided the best estimate of fish length. Consequently it was not possible to determine the true sizes of stoneloach ingested by otters using this method. However, the errors in fish size estimates were assumed to be the same in each season enabling an assessment of the relative seasonal changes in the size distribution of stoneloach in the diet. Table VI.VII in Appendix VI gives the frequencies and proportions of fish for each stoneloach length class for each season estimated from both caudal (a) and thoracic (b) vertebrae. The stoneloach length distributions derived from both caudal and thoracic vertebrae differed significantly between seasons (Friedman 2-way ANOVA = 14.4, 3df $p < 0.001$ for caudal vertebrae and 18.8, 3df, $p < 0.001$ for thoracic vertebrae). Multiple comparisons analyses (Table 4.3.7) showed that all seasons differed significantly from each other ($r(\alpha, k, n) = 15$ at $\alpha = 0.05$ and $r(\alpha, k, n) = 18$ at $\alpha = 0.01$). Examination of the length distributions for stoneloach in each season showed that for fish lengths derived from caudal vertebrae (Figure 4.3.8a) there was a single peak at size class 6 and 7 (>70≤90mm) in the Spring sample. This peak was also present in the Summer sample but there was an additional peak at size classes 3 and 4 (>40≤60mm). In the Autumn sample the majority of fish lengths were between size classes 3 and 5 (>40≤70mm) which is similar to the peak at smaller fish sizes found in the Summer sample. In the Winter there were two peaks at size classes 4 and 7 (>50≤60mm and >80≤90mm) although the results for this season should be treated with some caution due to the low sample size. For fish lengths derived from thoracic vertebrae (Figure 5.3.8b) a similar seasonal change was observed. In the Spring sample there was a single peak in the length distribution at size class 6 (>70≤80mm). In the Summer sample the majority of fish lengths were in size classes 5 to 7 (>40≤70mm) but there were also higher frequencies in the smaller size classes than in other seasons. In the Autumn

sample there was a single peak at size class 4 (>50≤60mm which was also observed in the Winter sample with an additional peak at size class 6 (>70≤80mm) as in the Spring sample.

Table 4.3.7 Friedman multiple comparisons test of the absolute differences, $|R_u - R_v|$, between seasons in the lengths of stoneloach estimated from caudal (a) and thoracic (b) vertebrae found in otter spraints collected during four seasonal surveys of the upper Tyne catchment between 1993 and 1994.

(a) Caudal

	u			
v	1 (Spring)	2 (Summer)	3 (Autumn)	4 (Winter)
1 (Spring)	-			
2 (Summer)	229**	-		
3 (Autumn)	115**	344**	-	
4 (Winter)	169**	398**	54**	-

** Significant at $p < 0.01$

(b) Thoracic

	u			
v	1 (Spring)	2 (Summer)	3 (Autumn)	4 (Winter)
1 (Spring)	-			
2 (Summer)	23**	-		
3 (Autumn)	314**	548**	-	
4 (Winter)	294**	528**	20**	-

** Significant at $p < 0.01$

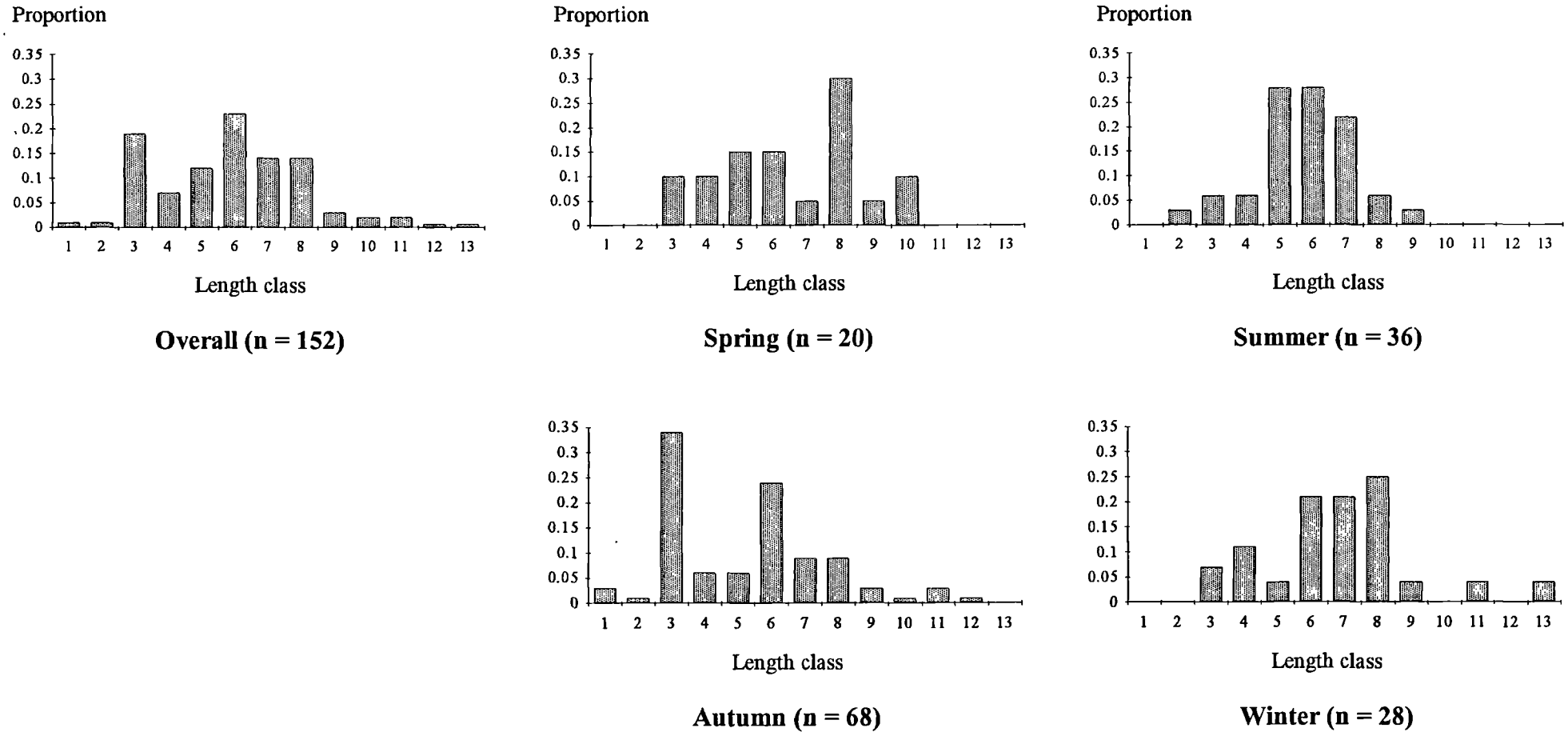


Figure 4.3.7 Distributions of minnow lengths in the diet of otters calculated from the gape measurement of pharyngeal bones found in spraints collected during four seasonal surveys of the upper Tyne catchment between 1993 and 1994.

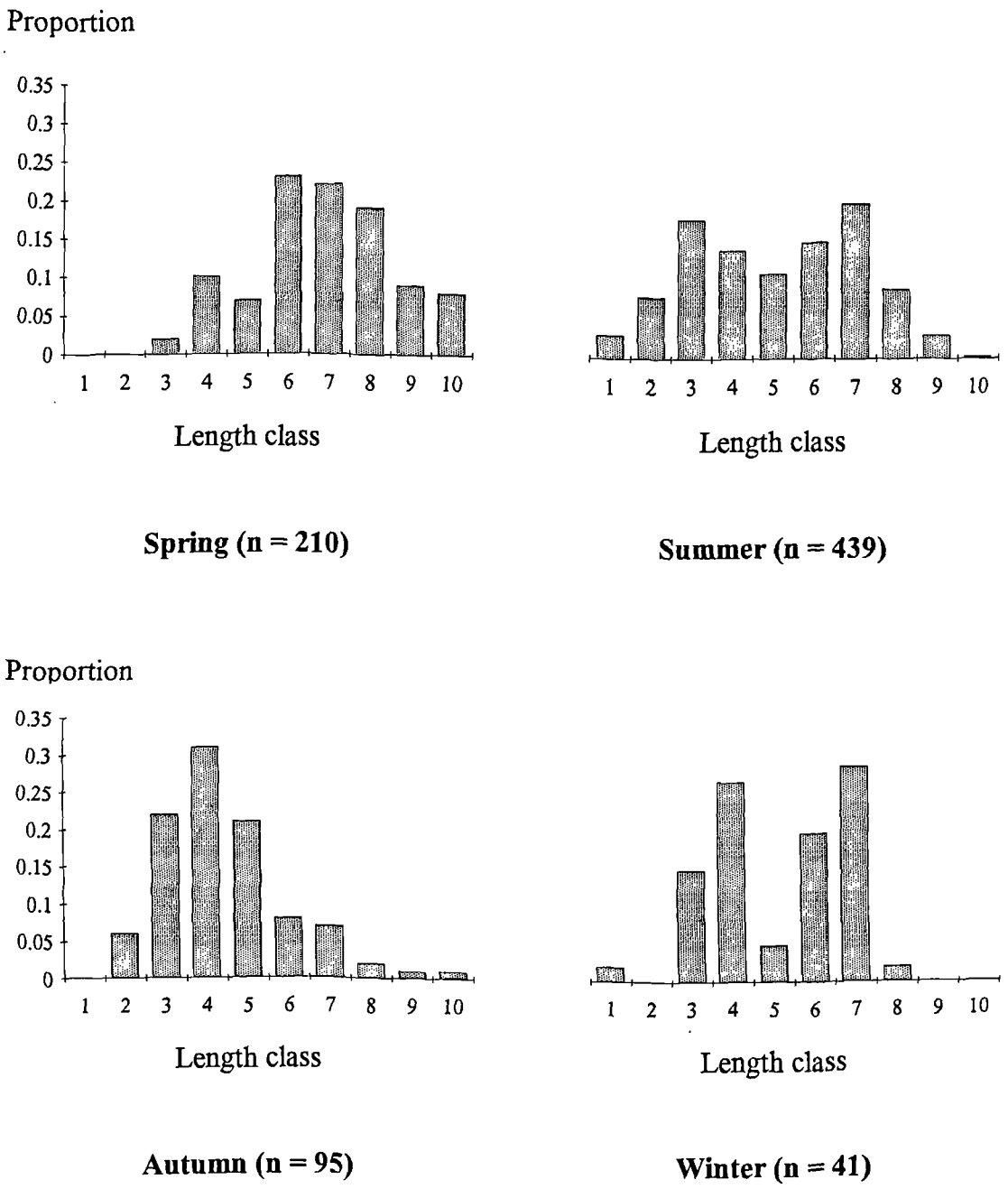


Figure 4.3.8a Distributions of the lengths of stoneloach in the diet of otters estimated from the lengths of caudal vertebrae found in spraints collected during four seasonal surveys of the upper Tyne catchment between 1993 and 1994.

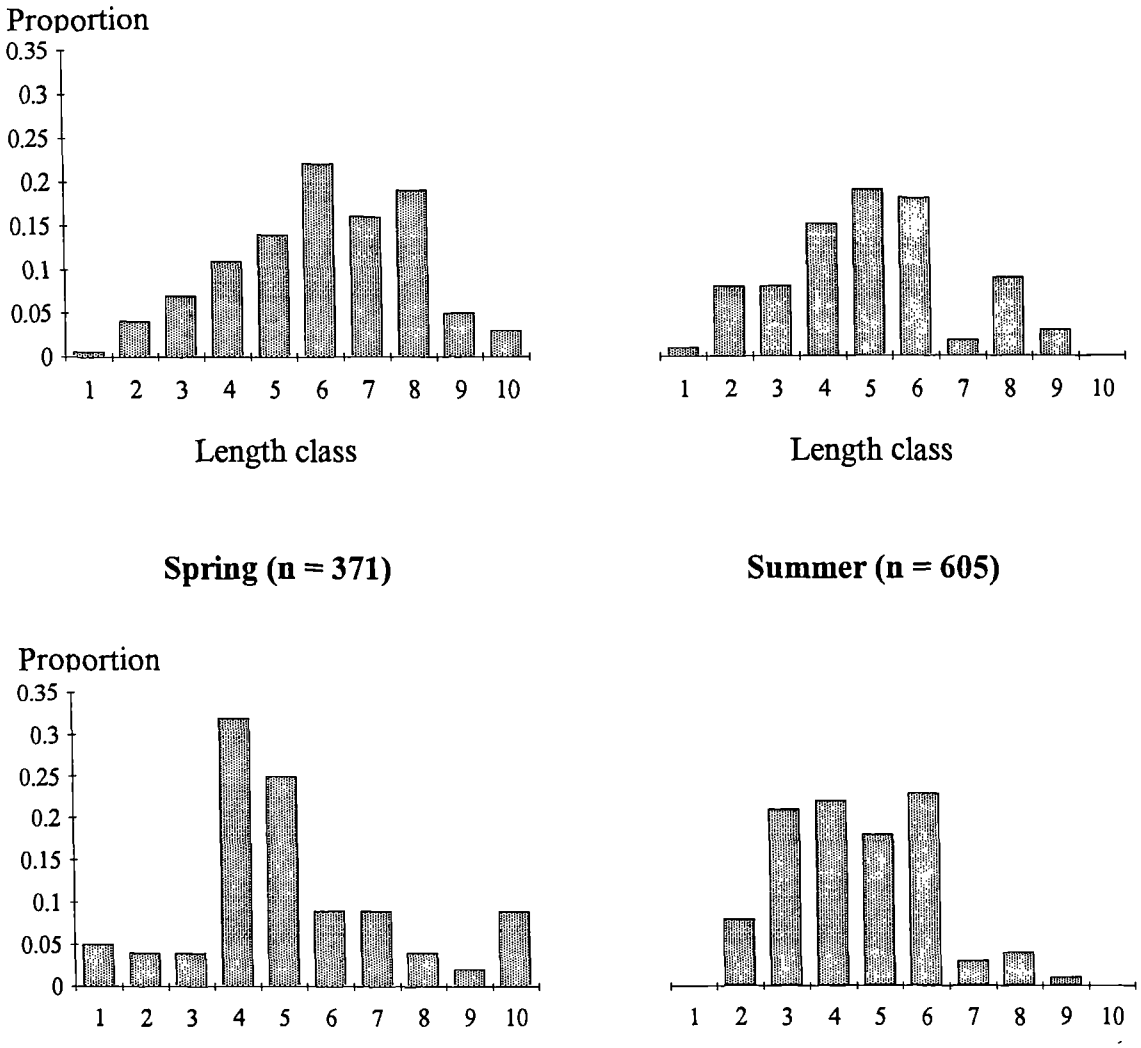


Figure 4.3.8b Distribution of the lengths of stoneloach in the diet of otters estimated from the lengths of thoracic vertebrae found in spraints collected during four seasonal surveys of the upper Tyne catchment between 1993 and 1994.

4.3.2 Electro-fishing

Population estimates

Table VII.I in Appendix VII gives the population estimates for each species caught at each site during the electro-fishing survey of the upper Tyne catchment in the summer of 1995. Ninety-five per cent confidence intervals are also given where these could be calculated. For trout, total salmonids and stoneloach the confidence intervals were sufficiently narrow to have reasonable confidence in the population estimates. For salmon, eels, stickleback, bullhead and lamprey confidence intervals could not be calculated due to the low numbers of fish caught at each site. For minnow, confidence intervals were calculated for some sites but these were so wide as to give little confidence in the population estimates at these sites primarily due to the shoaling behaviour of this species (Bohlin *et al.*, 1989). This lack of confidence in the population estimates of most species meant that the relative importance of different fish species in the total electro-fishing sample could not be calculated with any degree of accuracy using actual population estimates. To overcome this the 'percentage frequency' of each species in the sample was calculated in the same way as percentage frequency of each prey item in the diet, that is, the total number of sites at which the species was present was divided by the total number of electro-fishing sites (see 1995 column of Table 4.3.8). Confidence intervals were calculated from binomial sampling as for the spraint analysis. Salmonids formed the most widespread prey type (occurring at 84% of the sites) with trout being more widespread than salmon (84% and 32% of sites respectively). Stoneloach was the next most widespread species (68% of sites) followed by eel (62% of sites) and minnow (58% of sites). Lamprey, stickleback and bullhead were found at only a few sites.

It could be argued that the percentage frequency of fish in the 1995 electro-fishing sample was not representative of fish populations in previous years and could not, therefore, be used to compare with the diet of otters estimated from spraints collected in 1993 and 1994. However, the percentage frequency of each species was also calculated from National Rivers Authority and Newcastle University electro-fishing surveys of the same rivers and tributaries from 1991 to 1994 (NRA, 1991a, 1991b, 1992a, 1992b, 1994a & 1994b; Haile, 1992, 1993 & unpubl. data and Shelley, Ferry & Peacham 1993a,

1993b) (Table 4.3.8). It was found that the percentage frequency of all prey species (total salmonids not included in the analysis) did not differ significantly between years (Friedman 2-way ANOVA = 6.55, 4df, $p = 0.16$).

Table 4.3.8 Percentage frequency of fish species caught at 97 electro-fishing sites in the upper Tyne catchment between July and August 1995 compared with National Rivers Authority electro-fishing data from 1991 to 1994 (95% Confidence Limits, calculated from binomial sampling, in brackets)

Species	1991		1992		1993		1994		1995	
	sites	% freq. (n=21)	sites	% freq. (n=22)	sites	% freq. (n=37)	sites	% freq. (n=20)	sites	% freq. (n=97)
Trout	20	90(±13)	19	77(±18)	31	84(±12)	18	90(±13)	73	75(±9)
Salmon	19	48(±21)	17	59(±21)	31	35(±15)	18	40(±21)	31	32(±9)
Total salmonids	10	95(±9)	13	86(±14)	13	84(±12)	8	90(±13)	81	84(±7)
Stoneloach	14	67(±20)	10	45(±21)	12	32(±15)	10	50(±22)	66	68(±9)
Eel	9	43(±21)	13	59(±21)	14	38(±16)	12	60(±21)	60	62(±10)
Minnow	16	76(±18)	16	73(±19)	18	49(±16)	12	60(±21)	56	58(±10)
Lamprey	1	10(±13)	5	23(±18)	1	3(±5)	2	10(±13)	26	27(±9)
Stickleback	2	5(±9)	0	0	1	3(±5)	0	0	14	14(±7)
Bullhead	2	10(±13)	2	9(±12)	1	3(±5)	2	10(±13)	3	3(±3)

Fish size

Salmonids

Table VII.II in Appendix VII and Figure 4.3.9 show that salmon and trout length frequency distributions were bimodal with two distinct size groups between size class 1 and 5 (>30≤80mm) with a peak at size class 3 (>50≤60mm) and between size class 6 and 13 (>80≤160mm) with a peak at size class 8 (>100≤120mm). There was a highly significant difference between the salmon and trout length distributions (χ^2 = 148, 10df, $p<0.001$) caused primarily by higher numbers of trout in size classes greater than 130mm.

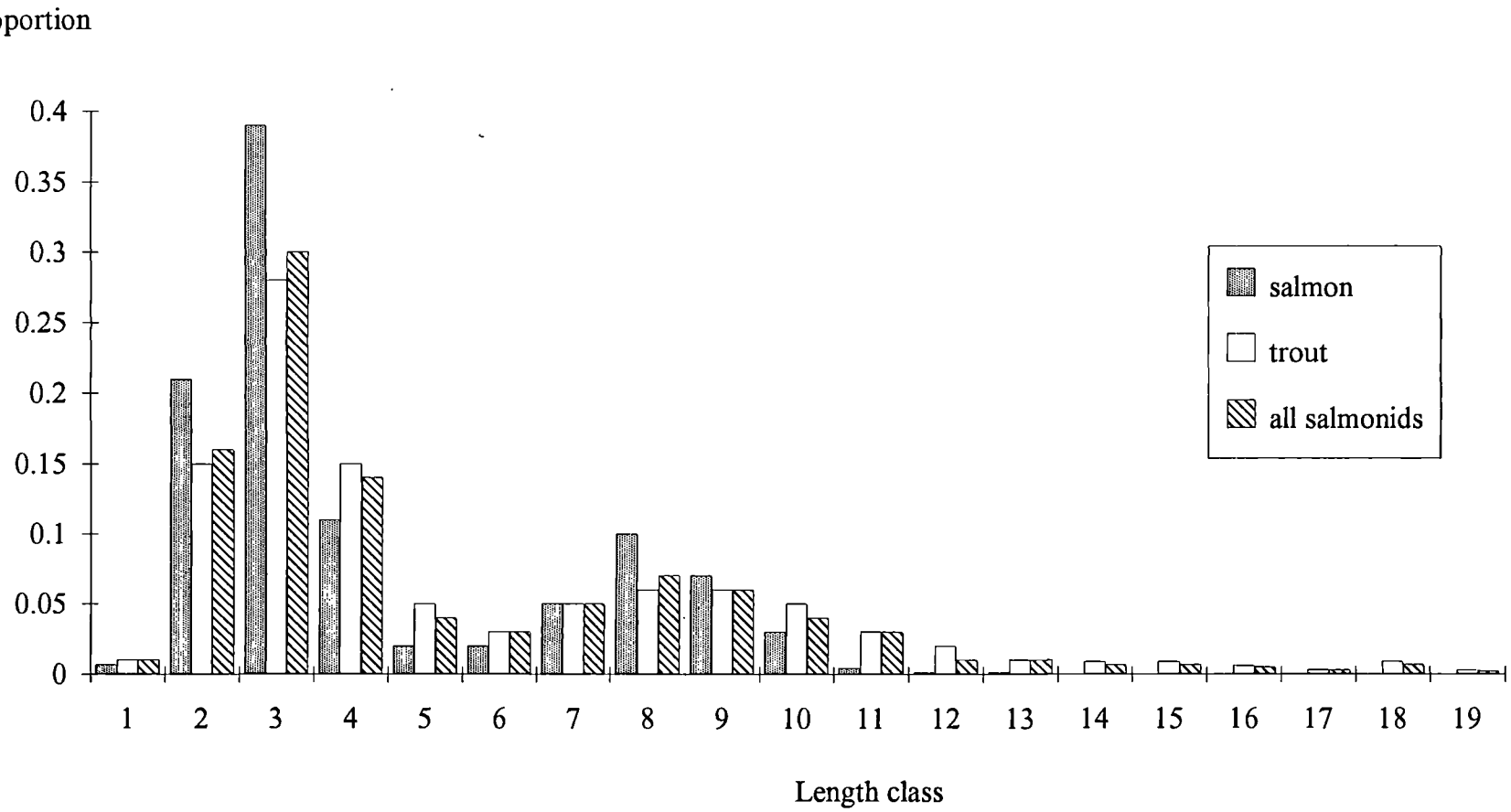


Figure 4.3.9 Distributions of all salmonid, salmon and trout lengths (n = 4007, 762 and 3245 respectively) measured during an electro-fishing survey of the upper Tyne catchment in the summer of 1995.

Other species

Table VII.III in Appendix VII and Figure 4.3.10 show that the eel length frequency distribution had a single mode with fish sizes ranging from 100mm to 700mm in length with a peak at size class 5 (>300≤350mm). The length frequency distribution for minnows (Table VII.IV in Appendix VII and Figure 4.3.11) also had a single mode with the majority of fish ranging from 30mm to 90mm in length with a broad peak between size classes 4 and 6 (>45≤60mm).

The length frequency distribution of stoneloach was bi-modal (Table VII.V in Appendix VII and Figure 4.3.12) with two size groups; (i) between size groups 1 and 10 (>30≤80mm) with a peak at class 7 (>60≤65mm); and (ii) between size classes 11 and 18 (>80≤155mm) with a peak at size class 13 (>90≤95mm).

Stickleback formed only a minor component of the otters' diet and lamprey and bullhead did not feature in the diet at all. In addition these three species were also at low density in the electro-fishing sample. Therefore, the length distribution of these species was not considered in this analysis.

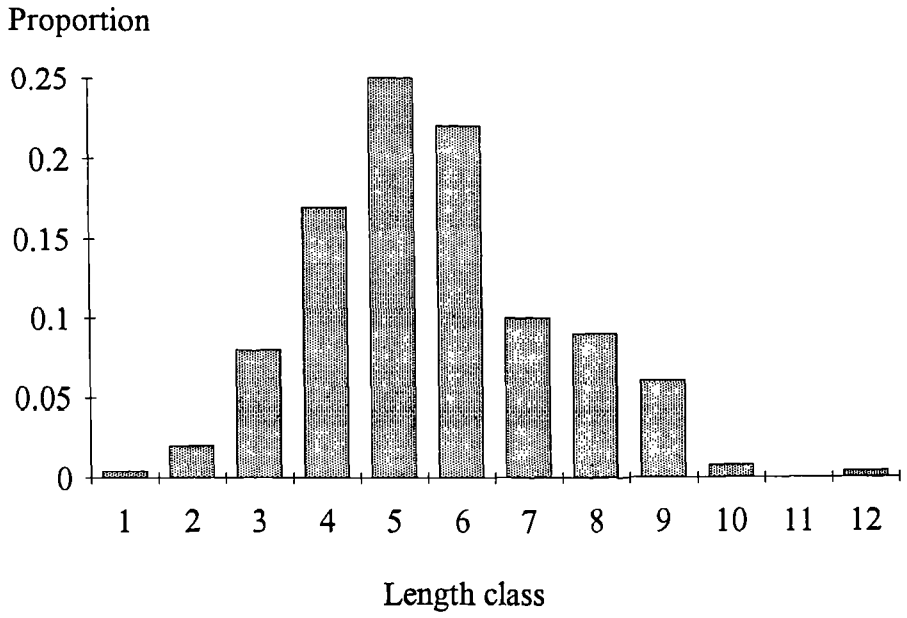


Figure 4.3.10 Distribution of the lengths of eels (n = 249) caught during an electro-fishing survey of the upper Tyne catchment in the summer of 1995.

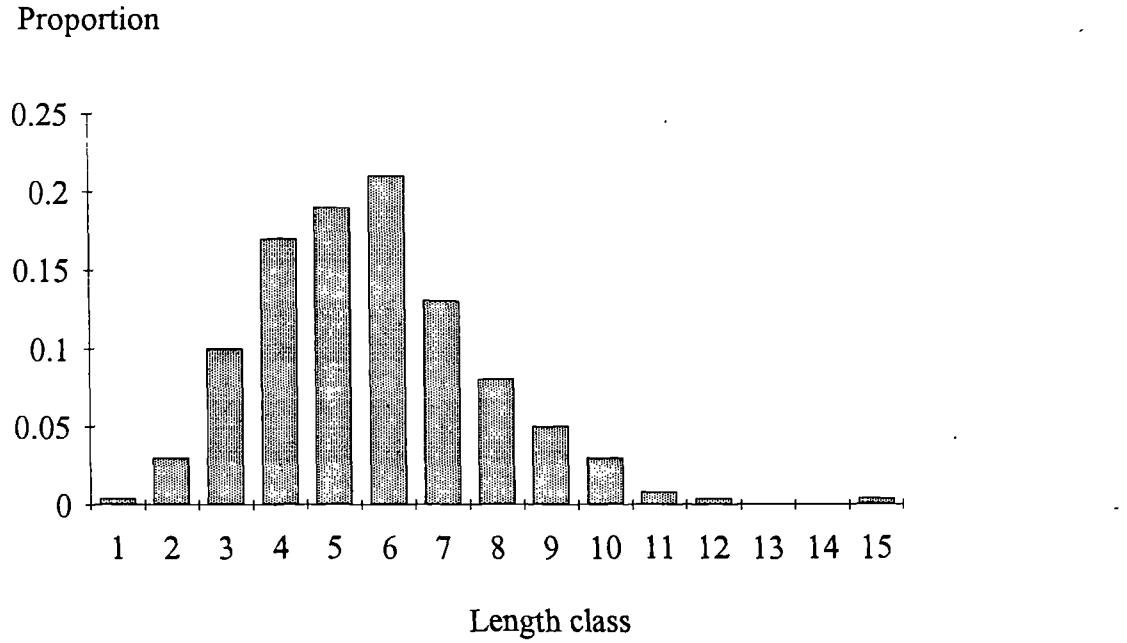


Figure 4.3.11 Distribution of the lengths of minnows (n = 1991) caught during an electro-fishing survey of the upper Tyne catchment in the summer of 1995.

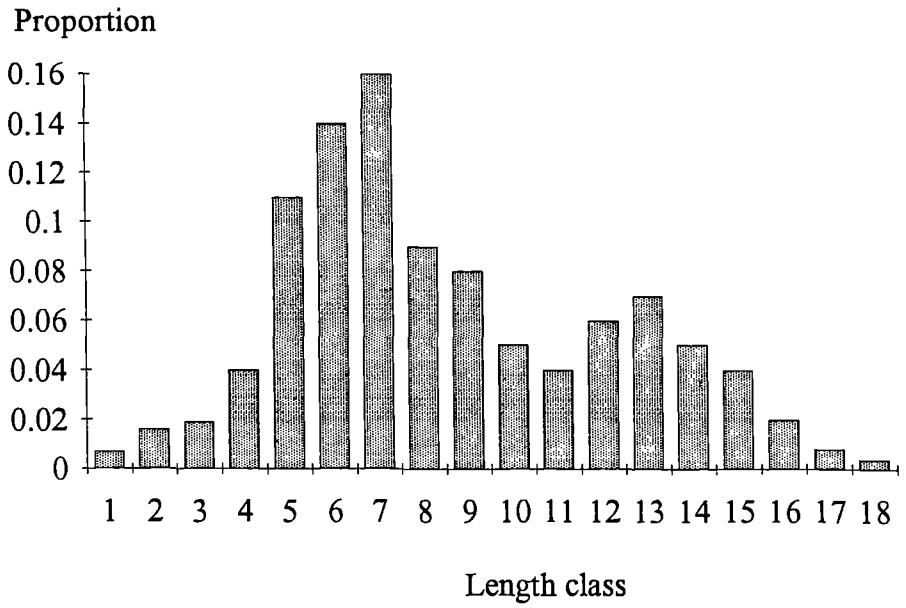


Figure 4.3.12 Distribution of the lengths of stoneloach (n = 1629) caught during an electro-fishing survey of the upper Tyne catchment in the summer of 1995.

4.3.3 Comparing otter diet with fish populations

Fish size

Since electro-fishing was conducted in the summer this section compares prey availability with diet in the summer only.

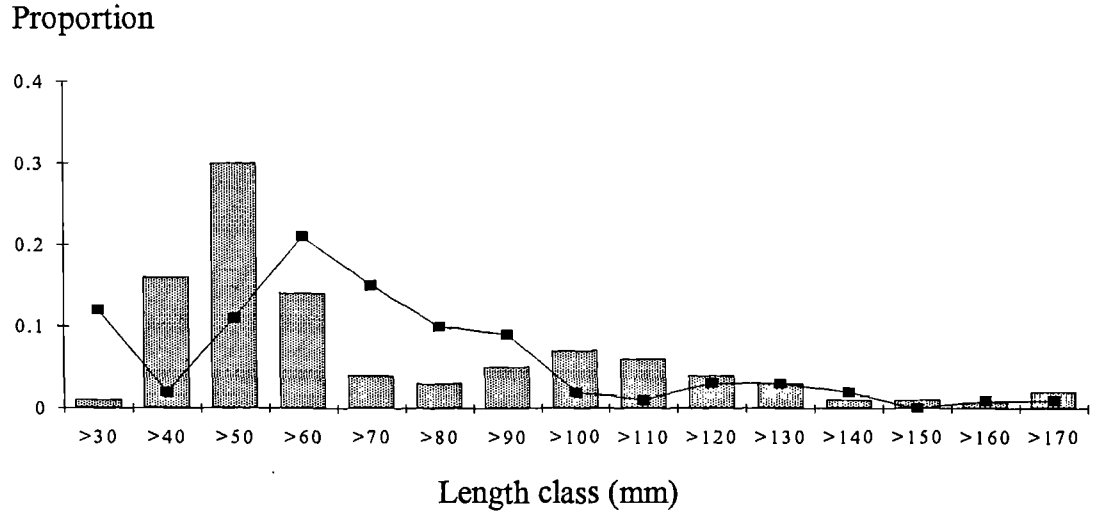
Salmonids

Figure 4.3.13 shows that there was a significant difference between the length frequency distributions of total salmonids, salmon and trout in the diet calculated from the size of atlas bones and the length frequency distribution of total salmonid, salmon and trout lengths measured during the electro-fishing survey (salmonids, χ^2= 105, 10df $p<0.01$; salmon, $\chi^2 = 75$, 5df, $p<0.01$ and trout, $\chi^2 = 59$, 6df $p<0.01$) with a higher proportion of fish in the diet in the >30≤40mm and >70≤90mm length ranges and a lower proportion in the >50≤60mm size class.

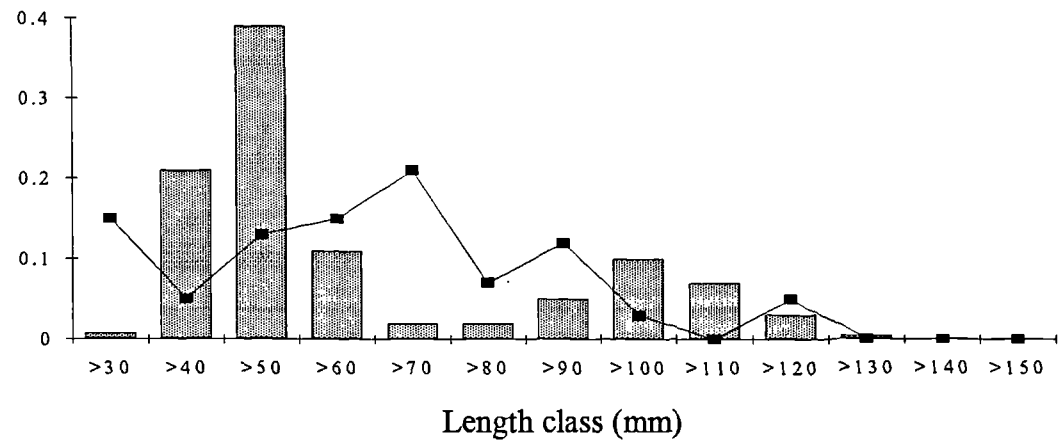
However, this analysis involved the comparison of the length frequency distribution for salmonids calculated from atlas bones which, due to small sample sizes, did not take seasonal differences into account. It may, therefore, be invalid to compare these data with the results of the electro-fishing sample which was conducted in the summer only. Therefore, the electro-fishing data were then compared with the summer salmonid length frequency distributions determined from the lengths of caudal and thoracic vertebrae. Any interpretations from this analysis should be treated with some caution since it is not known how representative the length estimates from these bones in faecal remains are of the sizes of actual fish ingested. Figure 4.3.14 shows that, for caudal vertebrae, there was a significant difference between the salmonid length distribution in the summer in the diet and the distribution found in the electro-fishing sample ($\chi^2 = 302$, 13df, $p<0.001$). There were higher numbers of fish in the diet in the >40≤50mm and >90≤100mm size classes with lower numbers of fish in the diet in the >50≤60mm size class which was similar to the distribution derived from the width of atlas vertebrae.

Similar results were obtained when the salmonid length frequency distribution in the electro-fishing sample was compared with the distribution determined from the lengths of thoracic vertebrae (Figure 4.3.15). There were significantly higher numbers of fish in the diet in the >70≤90mm size range and lower numbers in the >50≤60mm size class (χ^2 = 685, 13df, $p<0.001$) although no selection for the smallest size classes were observed as in the case of the length frequency distributions calculated from caudal vertebrae. It would appear therefore that otters take (and even select for) salmonids in the >70≤90mm size range with smaller fish (>40≤50mm) taken in the summer months when they are abundant.

(a) All salmonids



(b) Salmon



(c) Trout

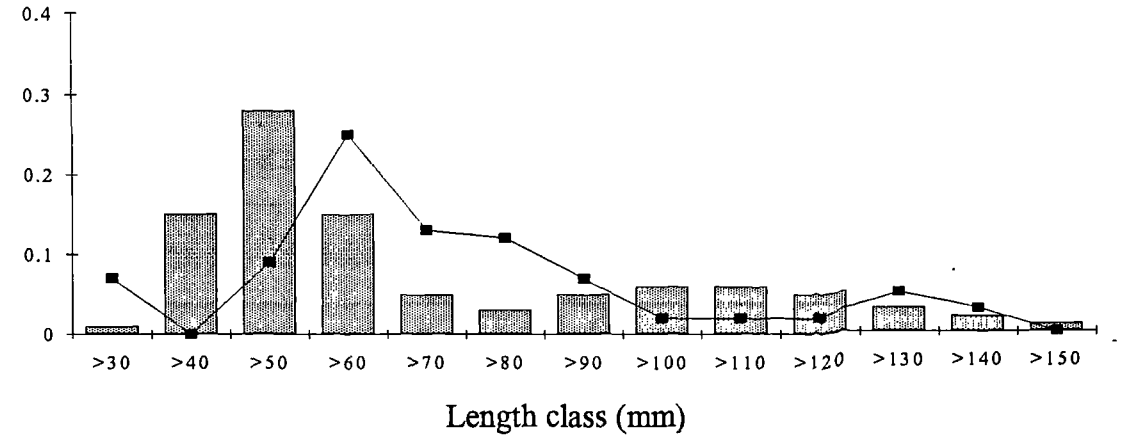


Figure 4.3.13 Comparison of the sizes of salmonids estimated from atlas bones found in otter spraints collected during four seasonal surveys between 1993 and 1994 (solid line) with fish caught during an electro-fishing survey of the upper Tyne catchment in the summer of 1995 (histogram).

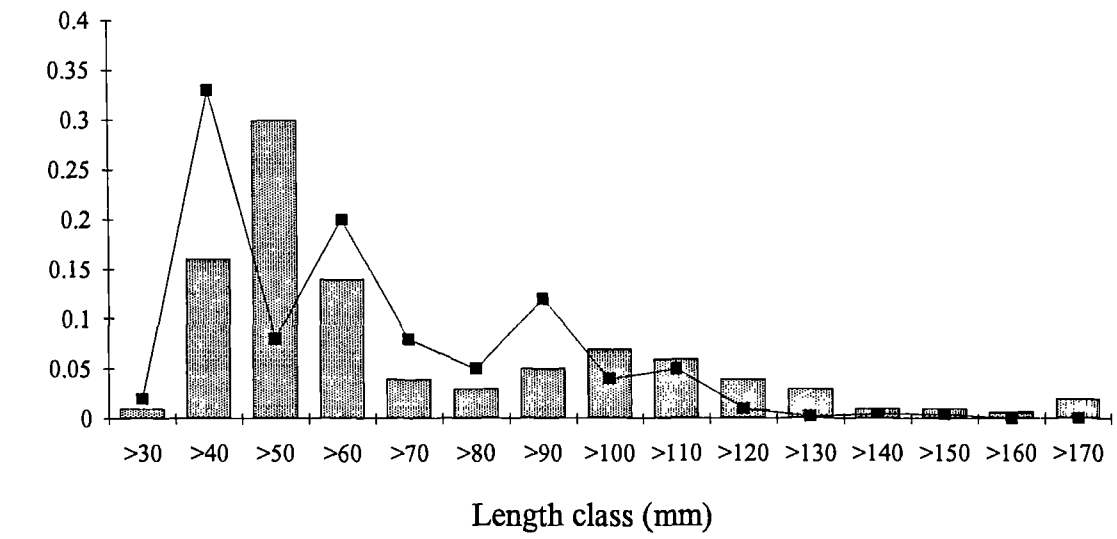


Figure 4.3.14 Comparison of the sizes of salmonid fish estimated from the size of caudal vertebrae found in otter spraints in the summer of1993 (solid line) with fish caught during an electro-fishing survey of the upper Tyne catchment in the summer of 1995 (histogram).

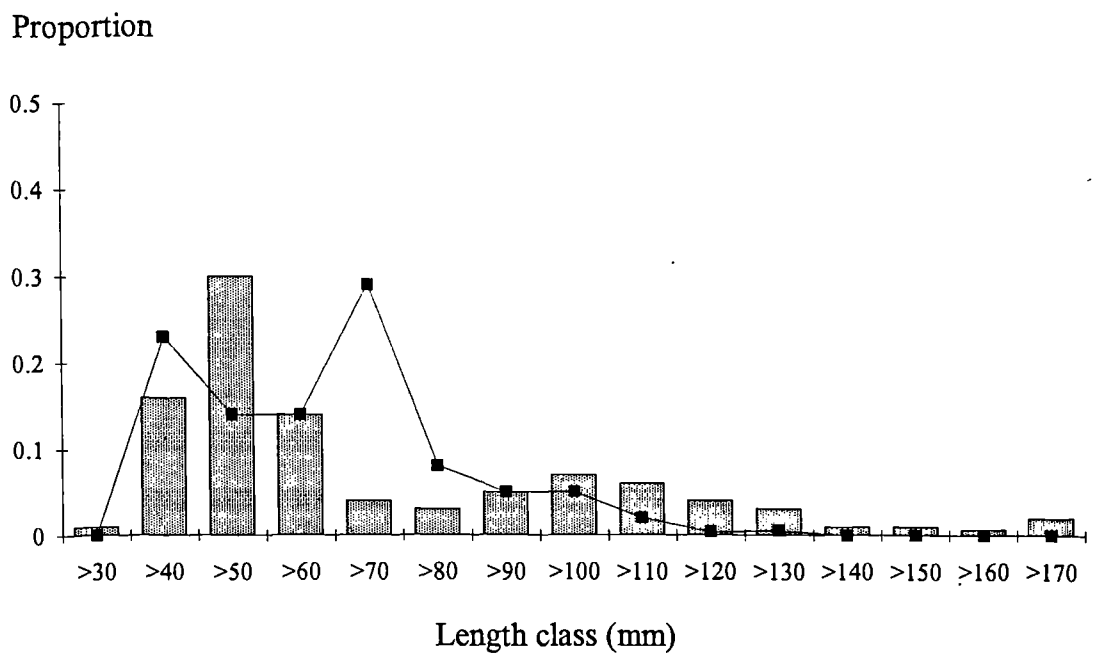


Figure 4.3.15 Comparison of the sizes of salmonid fish estimated from the size of thoracic vertebrae found in otter spraints in the summer of 1993 (solid line) with fish caught during an electro-fishing survey of the upper Tyne catchment in the summer of 1995 (histogram).

Eels

The length frequency distribution for eels determined from the length of thoracic vertebrae found in spraints collected in all surveys differed significantly from the distribution in the electro-fishing sample (χ^2 = 180, 7df $p<0.01$) with significantly higher numbers of fish in the diet in the >200≤250mm size class and lower numbers in the >500mm size class (Figure 4.3.16). The results for the summer sample showed that there was a significant difference between the length frequency distribution in the diet in the summer and the electro-fishing sample with the number of fish in the >200≤250mm size class significantly higher in the diet and a significantly lower proportion of fish in the >350≤350mm size class (χ^2 = 58, 7df, $p<0.01$).

Minnows and stoneloach

A comparison of minnow and stoneloach size distributions in the diet with the distribution in the electro-fishing sample was problematic for a number of reasons. First, unlike salmonids and eels, no feeding trials with captive otters have been carried out to determine whether minnow and stoneloach vertebrae show size-related differential recovery. Second, very small minnows and to a lesser extent small stoneloach were very difficult to catch during electro-fishing bouts due to their shoaling behaviour thus biasing the results towards larger size classes. Third, as was already shown in section 4.3.1, the stoneloach length frequency distribution estimated from caudal vertebrae differed signficantly from that estimated from thoracic vertebrae making it impossible to determine which vertebra type provided the best estimate of fish length. These problems should, therefore, be carefully considered when interpreting the following results.

The number of minnow pharyngeal bones recovered from otter spraints was too low to allow statistical comparisons of seasonal differences in the size distribution of fish in the diet with that in the electro-fishing sample. Figure 4.3.17 shows that in the summer diet the length distribution was skewed to the left of the distribution in the electro-fishing sample with higher numbers of fish in the >40≤55mm size range. It was probable therefore, that, otters took minnows mainly in proportion to availability but took a higher proportion of small fish when these were abundant. The shoaling behaviour of small

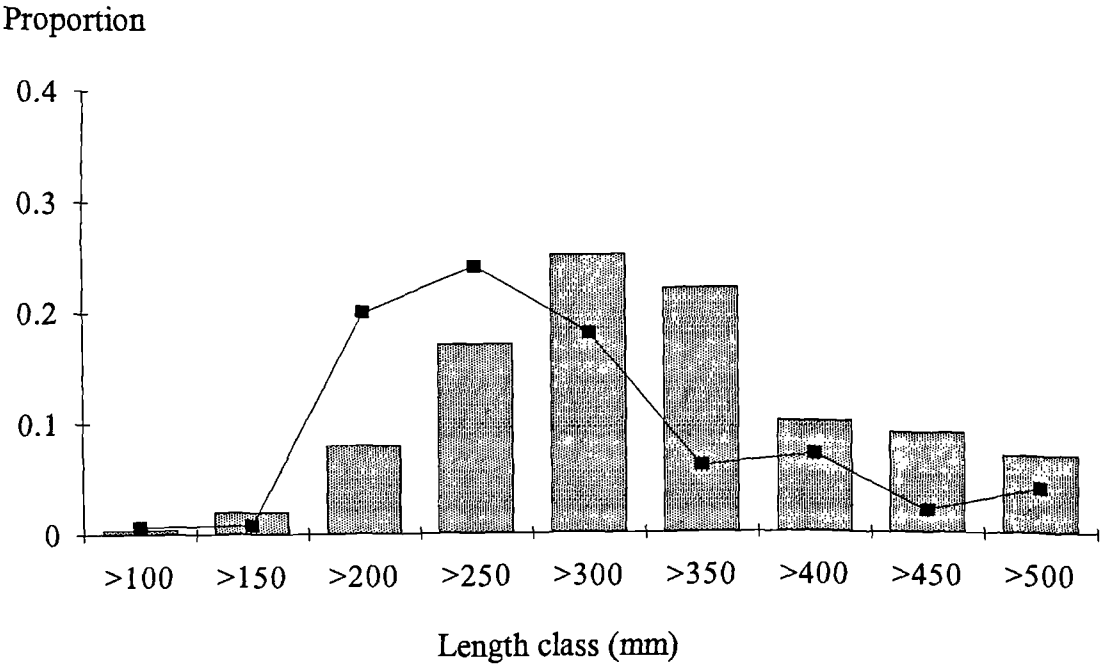


Figure 4.3.16 Comparison of the sizes of eels estimated from the size of thoracic vertebrae found in otter spraints in the summer of 1993 (solid line) with fish caught during an electro-fishing survey of the upper Tyne catchment in the summer of 1995 (histogram).

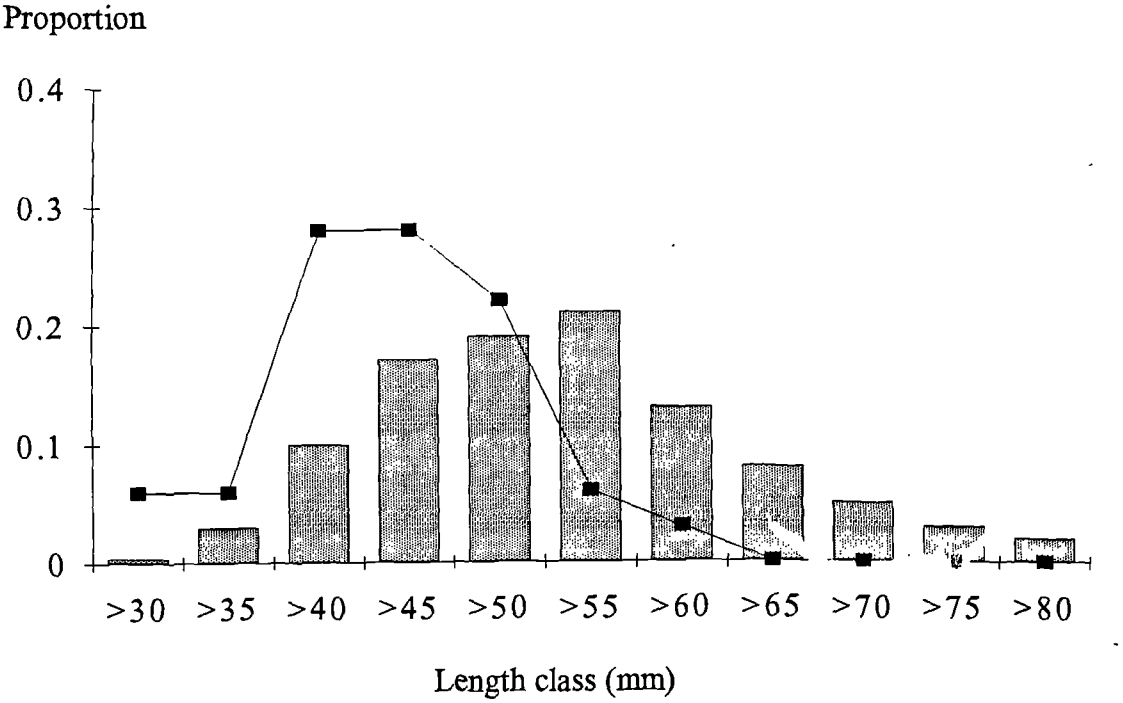


Figure 4.3.17 Comparison of the sizes of minnows estimated from the size of pharyngeal bones found in otter spraints in the summer of 1993 (solid line) with fish caught during an electro-fishing survey of the upper Tyne catchment in the summer of 1995 (histogram).

minnows may have made them more vulnerable to capture leading to increased predation from otters.

Since it was not possible to determine whether stoneloach caudal or thoracic vertebrae provided a good estimate of the size of fish ingested by otters statistical comparison of the length frequency distribution in the diet with that in the electro-fishing sample would have been invalid. However, Figure 4.3.18 shows that the fish length frequency distribution calculated from the lengths of caudal vertebrae found in spraints in the Summer differed from the distribution in the electro-fishing sample with two peaks occurring in the diet at >40≤50mm and >80≤90mm. The entire distribution appeared to lag behind the length frequency distribution in the electro-fishing sample by approximately one size class.

Figure 4.3.19 shows that the length frequency distribution calculated from the lengths of thoracic vertebrae showed a similar pattern although the bi-modality in the diet was not as apparent with the distributions broadly reflecting that of the electro-fishing sample. It is interesting to note that the two main size ranges of stoneloach in the diet (>40≤60mm and >80≤90mm) were similar to the two main size classes of salmonids (>30≤50mm and >70≤90mm) and to the size of the majority of the minnows (>30≤55mm) in the diet.

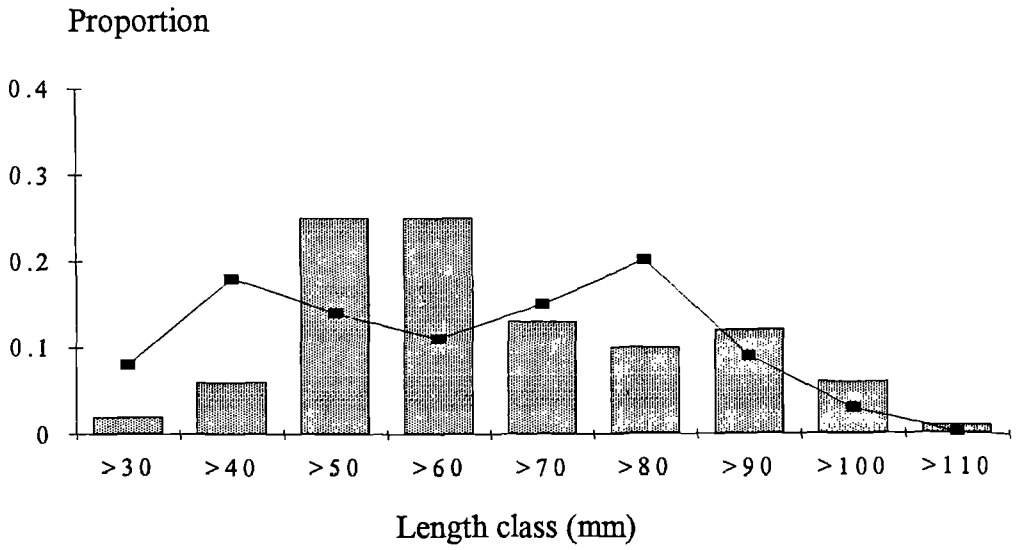


Figure 4.3.18 Comparison of the sizes of stoneloach estimated from the size of caudal vertebrae found in otter spraints in the summer of 1993 (solid line) with fish caught during an electro-fishing survey of the upper Tyne catchment in the summer of 1995 (histogram).

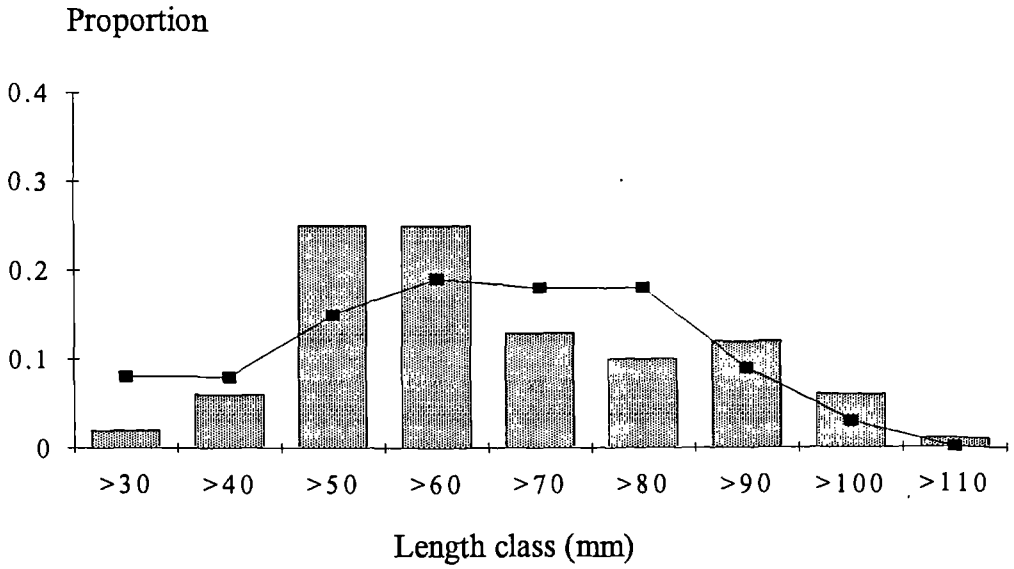
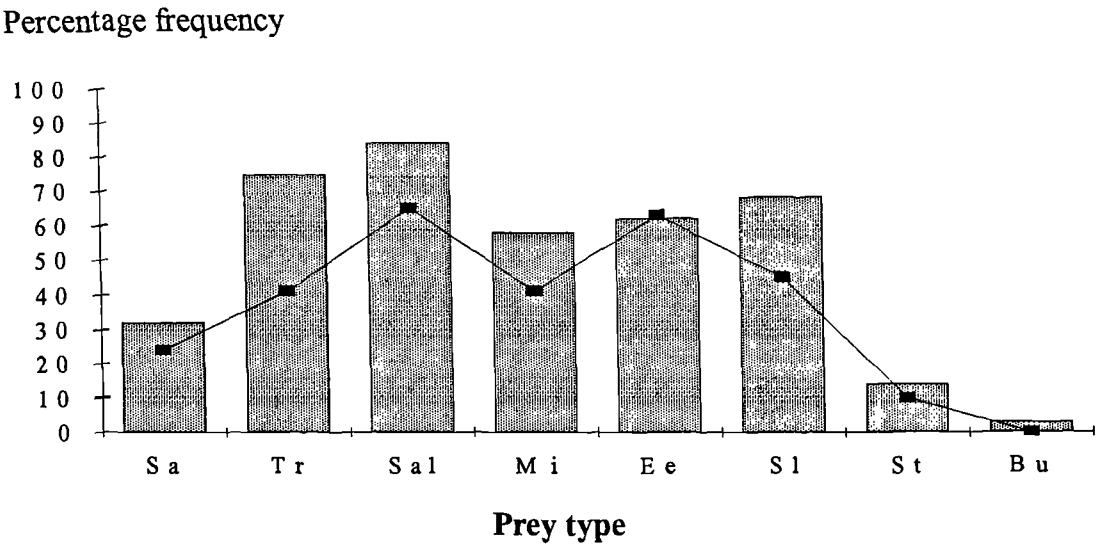


Figure 4.3.19 Comparison of the sizes of stoneloach estimated from the size of thoracic vertebrae found in otter spraints in the summer of 1993 (solid line) with fish caught during an electro-fishing survey of the upper Tyne catchment in the summer of 1995 (histogram).

Species composition of the diet compared with availability

Figure 4.3.20a shows the percentage frequency of each fish prey group in the summer diet compared with the percentage frequency of each species in the summer electro-fishing sample. The width of the 95% confidence limits and the errors associated with spraint analysis made statistical interpretations invalid. However, despite this, it can be seen that the percentage frequency of prey groups in the diet broadly reflected the electro-fishing sample with two possible exceptions. The proportions of stoneloach, trout and consequently, total salmonids, were lower in the diet than in the electro-fishing sample. However, if the percentage frequencies of the main size classes for these species (>30≤50mm and >80≤90mm for stoneloach and >70≤90mm for salmonids) were compared (Figure 4.3.20b) the percentage frequencies of these species in the diet more closely matched their percentage frequencies in the electro-fishing sample.

a.



b:

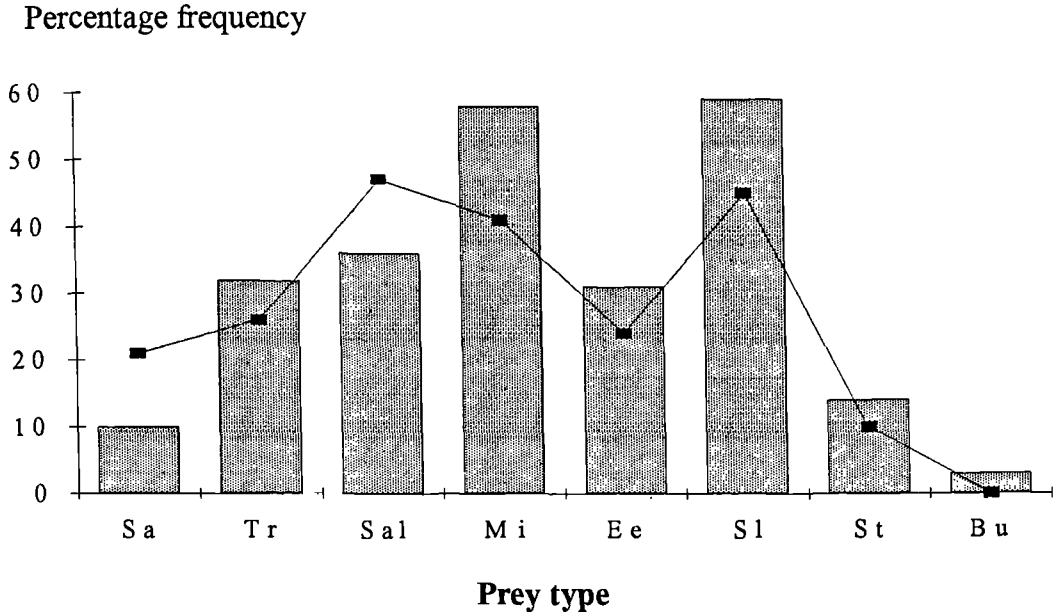


Figure 4.3.20a Comparison of the percentage frequency of each prey type encountered in spraints collected in the summer of 1993 (solid line) with the percentage occurrence of each prey type caught during an electro-fishing survey of the upper Tyne catchment in the summer of 1995 (histogram). **b** For salmonids, stoneloach and eels only the percentage frequency of certain size classes were compared which were shown to be the most important in the diet (>40≤50mm & >70≤90mm for stoneloach, >70≤90mm for salmonids and >200≤300mm for eels). Sa = Salmon, Tr = Trout, Sal = all salmonid, Mi = Minnow, Ee = Eel, Sl = Stoneloach, St = Stickleback, Bu = Bullhead.

4.4 DISCUSSION

Carss and Parkinson (1996) argued that the independence of estimates from individual spraints was questionable since their feeding trials showed that the remains of many prey items occurred in single spraints and also that the remains of a single prey item could occur in many different spraints. They pointed out that this would result in the importance of prey items being overestimated in studies where spraints were collected in the same geographical area from traditional sites that were regularly marked as in the majority of previous studies (Jenkins *et al.*, 1979; Jenkins & Harper, 1980; Wise *et al.*, 1981; McFadden & Fairley, 1984; Kemenes & Nechay, 1990; Kozena *et al.*, 1992 and Kruuk *et al.*, 1993). In the present study this problem was partially overcome by analysing only a small number of spraints randomly selected from each 5km stretch of the upper Tyne thus ensuring that the spraints were widely distributed and therefore more likely to be independent of each other. However, this did lead to smaller sample sizes which increased the width of the 95% confidence intervals in the frequency of occurrence estimates. However, despite these errors, a number of broad conclusions could be drawn about the diet of otters in the upper Tyne catchment which confirmed the findings of many previous studies. First, otters in the Tyne were almost exclusively piscivorous with 96-100% of all spraints containing fish remains which was typical of the findings of previous workers (see Table 4.1.1). Mammals and amphibians were the only other major prey types in the diet occurring in approximately 4-12% and 4-11% of all spraints respectively. Mammal remains were found at low levels in all seasons and it was likely that, if these remains had been identified to species, their importance in the diet would be further reduced since Carss & Parkinson (1996) showed that 15% of mammal remains in their study was otter fur presumably from grooming. Amphibian remains were found in spraints in Spring and Winter only. This seasonality had been observed by other workers (Erlinge, 1967b; Jenkins *et al.* 1979 and Weber, 1990) and was probably due to otters taking advantage of the congregations of amphibians in winter and spring for hibernation and spawning respectively. No large invertebrate remains were found in the spraints in any season although otters are known to actively prey on large *Dytiscus* spp. beetles (Jenkins *et al.* 1979; Foster & Turner, 1991 and Kozena *et al.* 1992). Crayfish were also absent from the diet of otters in the upper Tyne catchment. It was interesting to note that in many studies where they occur they become an important part of the diet (Erlinge, 1967; McFadden & Fairley, 1984; Adrian & Delibes, 1987; Kyne, Smal & Fairley, 1989

and Thom, 1989) with otters changing their feeding habits in response to the introduction of crayfish into habitats where they did not previously occur (Delibes & Adrian, 1987). Crayfish (*Austropotamobius pallipes*) were once abundant in some localities of the upper Tyne catchment (Brewis & Bowler, 1983) but electro-fishing surveys in recent years failed to find any evidence that they still occur and there is concern that the species may be under threat in these areas (NRA, 1995). Of the fish prey encountered salmonids formed the largest proportion of the diet overall with trout constituting a higher proportion than salmon. Minnows, eels and stoneloach constituted similar proportions of the diet overall when percentage frequency was used although minnows and stoneloach formed a greater proportion than eels when relative frequency was used. When the salmonids were divided into salmon and trout minnows were as important as trout in the diet. There were, however, some seasonal fluctuations in the relative proportions of different prey groups in the diet. Salmonids formed the largest component of the diet in all seasons with eels being equally important in the summer. However, minnows were as important as trout in the summer and autumn. It was apparent that, for salmonids, there was a general pattern of low percentage frequency in the summer and high in the winter. The percentage frequencies of eels and stoneloach in the diet also showed a marked seasonal fluctuation being highest in the summer and lowest in the winter.

The almost exclusively piscivorous habit of otters with salmonids predominating and the seasonal fluctuation in the occurrence of some prey species in the present study confirmed the findings of many previous studies of otter diet in riparian habitats. Jenkins & Harper (1980) found that salmonids dominated the diet of otters from the River Dee, Aberdeenshire occurring in significantly higher proportions in the winter months. They also showed that the occurrence of eels was higher in the summer when the occurrence of salmonids was lower although their 95% confidence intervals were wide casting doubt on the statistical significance of these differences. The occurrence of all other species was considered to be low and unimportant. They concluded that the seasonal fluctuation in the occurrence of eels in the diet was due to a change in eel behaviour in the winter months when they remain torpid in the bottom substrate. Wise *et al.* (1981) also demonstrated the importance of salmonids which formed the most important component of the diet in autumn and winter in the Rivers Dart and Webburn, Devon with eels being more important in the spring and summer. They argued that eels were more susceptible

to predation in the summer because they were active and slower-moving than other species (Bainbridge, 1958). In addition, as eels were inactive in the winter, they were a less attractive prey item to otters since they prefer to hunt moving prey (Erlinge, 1968). Kruuk *et al.* (1993) showed that 90% of occurrences of prey in the diet of otters on the Beltie Burn and 87-89% on the River Dee, Aberdeenshire consisted of salmonids. They also showed that 82% of the salmonids eaten in the Beltie were trout compared to only 18% salmon. Eels were the only other important component of the diet, occurring in 45-62% of spraints from the Dee. In the present study, salmonids were an important component of the diet but other species, particularly minnows, were equally important in some seasons.

There have been few studies of otter diet that have compared the results obtained from spraint analysis with actual prey populations. Erlinge (1967b) concluded that, on the whole, otters took prey in proportion to abundance and that seasonal changes in the prey composition of the diet generally reflected seasonal changes in the abundance and behaviour of prey in the environment. However, no statistical evidence was given to confirm these conclusions and no information was given on confidence limits associated with the different prey estimation methods. Wise *et al.* (1981) also concluded that the prey composition of the diet reflected the abundance and availability of different species in the environment but again little statistical evidence was given to confirm these conclusions. Kruuk *et al.* (1993) concluded from their results that salmonids were the only important prey type in the Beltie and that otters consumed a considerable proportion of the biomass of these species. They also argued that salmon were more vulnerable to predation than trout since 17.7% of the salmonid atlas bones found in spraints were from salmon which was higher than in the electro-fishing sample where salmon constituted only 6.5% of the salmonid biomass. However, although it was stated that 95% confidence intervals were calculated for their electro-fishing population estimates these were not given. In the present study 95% confidence intervals were so wide for a number of species that exact population estimates were meaningless. In addition, for species which occurred in low numbers (e.g. salmon and eels), confidence intervals could not be calculated at all and therefore the accuracy of population estimates was unknown. Bohlin *et al.* (1989) suggested that the accuracy of population estimates from electro-fishing was often dependent on the behaviour of individual species with shoaling fish (e.g. minnows) and bottom-dwelling fish (e.g. eels) being extremely difficult

to quantify. Therefore, the accuracy of the population estimates calculated from just six electro-fishing sites and the subsequent conversion by Kruuk *et al.* (1993) into biomass estimates may be questionable. In the present study the results of the electro-fishing survey were converted into percentage frequency as for spraint analysis to allow a broad comparison of the relative importance of various species in the diet with that in the environment. There were errors associated with this method in that species that were widespread but occurred in low numbers at each site (e.g. eels) were probably over-represented and species that occurred in high numbers at a number of sites (e.g. minnows) were under-represented. However, it was considered that despite these errors the method did provide a broad estimate of the relative importance of each species in the upper Tyne catchment. These findings should, however, be treated with caution particularly in the light of the additional errors associated with spraint analysis (Carss & Parkinson, 1996). The conclusions of the present study broadly confirmed previous studies showing that prey types were taken in approximate proportion to availability with bottom dwelling species (eel and stoneloach) forming a lower proportion of the diet in the Winter because of their habit of remaining torpid in the bottom substrate during this period.

This study is one of the first to utilise equations developed by Carss & Elston (1996) for modelling size-related differential recovery of salmonid atlas bones and eel thoracic vertebrae to determine the size distribution of prey consumed by otters in a natural situation. It was found that otters in the upper Tyne catchment took salmonid prey mainly in the >70≤90mm length range regardless of season and in higher numbers than they were available in the habitat indicating positive selection for this size. This size class was similar to that found by Jenkins *et al* (1979) (9.5-17cm), Jenkins & Harper (1980) (7-12cm), Wise *et al.* (1981) (6-12cm), McFadden & Fairley (1984) (6-12cm) and was identical to the findings of Kruuk *et al.* (1993) who also used salmonid atlas bones in their analyses but without corrections for size-related differential recovery. The results of the present study also agreed with their findings that, on the whole, otters seemed to ignore small fry although it was possible that otters were taking smaller fish in the summer months. This conclusion was, however, tentative because the low recovery of salmonid atlas bones (Carss & Elston, 1996) led to a reduced sample size preventing seasonal comparisons of fish sizes. Caudal and thoracic vertebrae had to be used instead which provided less reliable estimates of prey sizes. Adrian & Delibes (1987) also

demonstrated that otters did take small fish, finding large numbers of mosquito fish (*Gambusia affinis*) in spraints collected from the Guadalquivir marshes in Spain. Carss & Elston (1996) also showed that even despite corrections for differential recovery small atlas bones were under-represented in the spraints due to complete digestion and the presence of large numbers of small minnow in the diet in the present study also tended to confirm that otters may indeed take small fish. The sizes of stoneloach ingested by otters in the upper Tyne was difficult to determine since the accuracy of fish lengths estimated from stoneloach caudal and thoracic vertebrae was unknown. However, it was found that two size ranges were important (>40≤60mm and >80≤90mm) which were very similar to the sizes of salmonids and minnows in the diet suggesting that these sizes may be the optimum prey size for these species. For eels the majority of fish in the diet were in the >200≤350mm length range with positive selection overall for fish in the >200≤250mm size class. This selection was also apparent when summer diet was compared with the electro-fishing sample while in other seasons the sizes of fish in the diet broadly reflected the electro-fishing sample. However, sample sizes were small in all cases so these conclusions should be treated with caution. Jenkins *et al.* (1979) and Jenkins & Harper (1980) found that the majority of eels in the diet of otters from the River Dee were in the 23-32cm size range which was similar to the findings in the present study. Wise *et al.* (1981) found that this size class was the most common for eels in the diet of otters on the Webburn and Dart in Devon and found no size selection when the length distribution was compared with eels caught during an electro-fishing survey.

The absence of large fish in the diet of otters from the Tyne catchment was surprising particularly since Carss *et al.* (1990) found that otters consumed large numbers of adult salmonids particularly during the spawning season in the winter. This lack of large salmonids in the diet may be due to a number of reasons. First, the remains of larger fish may not appear in spraints if the otter only eats a small proportion of flesh which contains no hard parts. Carss *et al.* (1990) showed that no bones were ingested at 51% of salmonid kills. However, that still left 49% of fish where bones were ingested. A second reason may be that many large migratory salmonids did not move into the upper reaches of the river during the study period. Wise *et al.* (1981) suggested that during warm summers with low water levels migratory salmonids remained in the estuaries and

did not move up to the spawning grounds in the upper reaches of the river. Concern was expressed by anglers during the present study that warm summer weather and low flow conditions were preventing fish from moving upstream and were leading to deaths of significant numbers of migratory fish in the Tyne estuary providing a possible reason for the lack of large salmonids in the diet of otters in this study.

5 PREDICTING THE SPATIAL DISTRIBUTION OF OTTER SIGNS IN THE UPPER TYNE CATCHMENT.

5.1 INTRODUCTION

There are a number of factors which could affect the spatial distribution of otters in a riparian environment. Environmental factors include physical characteristics of the river, availability of suitable riverbank cover, availability of resting and breeding sites, prey availability, pollution and the degree of human disturbance. In addition, social and reproductive behaviour of otters themselves may also influence their spatial distribution. It has been suggested that the function of otter spraints may be to signal the use or availability of resources (Kruuk, 1992) to conspecifics. If this is the case then it should be possible to predict the distribution of otter spraints from the distribution of environmental resources and consequently determine which areas of a river catchment provide suitable conditions for otters. If, on the other hand, otter sprainting is solely a function of social or reproductive behaviour then it is unlikely that spraint distribution will be predictable from environmental factors alone. The purpose of this chapter is to determine the degree to which the spatial distribution of otter spraints, and by implication the distribution of otters, in the upper Tyne catchment is predictable from environmental parameters.

5.1.1 Factors affecting the distribution of otters in riparian environments.

Physical characteristics of watercourses

Few studies have considered the relationship between otter distribution and physical characteristics of watercourses, such as river width, depth, substrate type or altitude.

Kruuk *et al.* (1993) showed that radio-tracked otters on the River Dee in Aberdeenshire, Scotland spent more time per length of river section along wider streams. If expressed as the amount of time otters spent per unit area of water, an exponential decrease was found in otter use per hectare of water with the width of the river. Kruuk *et al.* (1993) argued that this relationship was due to the higher fish densities in narrow streams, but

only eight otters were used in generating this relationship, five of these occupying rivers of a mean width of less than 10m and only two of greater than 50m. The significance of these relationships is therefore questionable given such small sample sizes. Secondly, Durbin (1993) showed that otters foraged close to or under banks, so that it may be more appropriate to consider otter activity per unit length of riverbank rather than total area of water. Dubuc *et al.* (1990) showed that the distribution of *Lutra canadensis* on Mount Desert Island, Maine could be predicted in part by the diversity of the riverbank structure which gave an indication of the amount of shallow foraging habitat available.

Durbin (1993) also showed that otters preferred sections with riffles, large boulders and/or gravel to areas with sandy or muddy substrates. Kruuk (1995) suggested that this was due to the distribution of salmonid fish, implying that otters preferred riffle areas because of the presence of large salmon (Carss *et al.,* 1990). However, it may also be that these substrate types hold higher numbers of smaller salmonids (Raleigh *et al.*, 1986) which are more important in the otter's diet than the large migratory salmonids. Durbin (1996) argued that the availability of high densities of small salmonids was particularly important when otter cubs were present.

Altitude may also play an important role in determining otter distribution. Melquist & Hornocker (1983) showed that *L. canadensis* in Idaho preferred valley habitats to mountainous ones suggesting that this may be particularly the case in winter when lakes and streams at high altitudes were inaccessible due to ice cover. Kruuk (1995) argued that in order to forage in cold water otters become active on land raising their body temperature prior to a foraging bout. At high altitude winter temperatures may be too low for otters to maintain normal body temperature particularly if foraging is difficult due to lack of access or inactivity of prey. Therefore, thermoregulatory constraints may restrict otters to lower altitudes during cold climatic conditions.

Riverbank vegetation

The majority of studies of otter ecology based on spraint density surveys have shown a positive relationship between spraint density and the amount of woody vegetation along the riverbank (Macdonald, Mason & Coghill, 1978; Jenkins & Burrows, 1980; Macdonald & Mason, 1983; Bas *et al.*, 1984). Kruuk *et al.* (1986) found for a

population of otters on the coast of Shetland, however, that there was no demonstrable relationship between the time spent in a particular habitat and spraint density. Their study area was a short stretch of rocky coastline which was known from previous studies to produce the highest densities of otters along the Shetland coast (Kruuk *et al.*, 1989) and where spraints were more common than in other habitats (Jenkins & Conroy, 1981). Within this study area 330m long units of coastline were compared for otter activity and levels of sprainting. It is possible that the habitat was not significantly different between these sampling units and therefore no differences in sprainting would have been expected if spraint density was an indicator of habitat utilisation. In a later study, Conroy & French (1987) showed that, using 2km sample units over 40km of coastline there was a relationship between the number of otters seen and the number of spraints found.

There is also some evidence from studies using radio-telemetry that supports the relationship between otter activity and bankside vegetation. Jefferies, Wayre, Jessop & Mitchell-Jones (1986) showed that radio-tracked otters spent over 50% of their time in wooded areas, although only a few individuals were tracked. Green *et al.* (1984) showed that one of their radio-tracked otters, but not a second, sprainted more at centres of activity which were in areas which were more wooded than elsewhere. Melquist & Hornocker (1983) who tracked a total of 39 *L. canadensis* in west central Idaho found that, in addition to food, otters required adequate "escape cover" in the form of dense riverbank vegetation. In the winter, snow and ice cover also provided shelter to dispersing otters. They argued that this was why otters preferred stream-related habitats to lakes, reservoirs and ponds in their study area. Durbin (1993) failed to show any relationship between otter activity and riverbank vegetation, showing instead a preference for rocky substrates. However, this study was conducted on only three otters for relatively short periods of tracking. It was shown, however, that cubs spent more time in stretches with overhanging vegetation (mainly alder, *Alnus glutinosa*) and boulder substrates which may have been associated with high densities of salmonid fishes (Durbin, 1996).

Availability of holt sites

A number of studies have suggested that the relationship between the distribution of otter signs and riverbank vegetation reflected the need for resting or holt sites which are

primarily in the root systems of bankside trees such as ash (*Fraxinus excelsior*) and sycamore (*Acer pseudoplatanus*) (e.g. Macdonald *et al.*, 1978; Macdonald & Mason, 1983). Harper (1981) described three holts which were in cavities below alder trees in areas that were safe from flooding along small secluded tributaries. Green *et al.* (1984) described a variety of different holt sites, the majority of which were in natural cavities. Holts situated under single trees were more common in lowland areas while elsewhere they were found in the roots of a number of trees or in a complex of tree roots and boulders. They also described other above-ground resting sites (couches), which were found in a variety of habitats ranging from substantial stickpiles, scrub-covered islands to simple depressions in bankside vegetation. Females preferred more secluded holt sites to males who would often rest in very exposed areas. Durbin (1996) showed that one female with cubs used 13 different holts in a 5.5km stretch of river, changing holts every two days. He argued that this may serve to familiarise the cubs with their home range and allow the female to exploit different resources. The number of holt sites in a short stretch of river may therefore be important during the early stages of cub growth. Kruuk (1995) suggested that holts were not important to otters in riparian environments although they were more likely to use them in winter. He argued that the use of holts by *L.canadensis* studied by Melquist & Hornocker (1983) in Idaho was also unimportant. However, this appears to be a wrong interpretation of their data since Melquist & Hornocker (1983) showed that sites providing protection and seclusion were preferred with beaver dens the most popular because of their availability and because they provided shelter with an underwater escape route. It is clear that the use of holt sites by otters is poorly understood but that they may be important at different times such as during breeding or in the winter months. Therefore, any study of otter habitat requirements needs to take account of the availability of holt sites.

Prey availability

As was discussed in chapter 4 very few studies of otter ecology have assessed the effects of prey availability on otter distribution. Kruuk *et al.* (1993) argued that because the use of streams by otters was correlated with fish biomass then it was probable that otter utilisation and otter numbers were food-limited. This may indeed be the case in the Dee catchment where the fish fauna is dominated by salmonids. However, in many studies other species such as bullhead, stoneloach, eel and cyprinids form significant

components of the diet (Jenkins & Harper, 1980; Wise *et al.*, 1981; Adrian & Delibes, 1987; Thom, 1989; Kozena *et al.*, 1992). In chapter 4 of this thesis it was shown that species such as minnow and stoneloach occurred in the diet with a higher rank order than trout and salmon when considered separately in some seasons (Figure 4.3.2). It is possible therefore that other fish species may provide an alternative prey source in those rivers and streams where salmonid biomass is limited.

Melquist & Hornocker (1983) showed that otters were able to adapt their foraging strategies to suit habitat type and thus exploit different prey in different areas. In small, shallow streams otters were observed foraging under banks and among obstructions to catch fish sheltering to avoid predators. In larger streams with deep pools otters generally foraged along log-jams situated in deep slow-moving water. In lakes with few slow-moving fish, otters foraged mainly along the shoreline, while in lakes with slow-moving fish, such as brown bullheads (*Ictalurus nebulosus*), otters foraged along the shoreline where fish were captured by direct pursuit. They also showed that high numbers of small fish, in particular cyprinids, were caught throughout the year. Peaks in the predation of small cyprinids in their study area coincided with a drop in the use of salmonids and suckers (*Catostomus macrocheilus*). It was argued therefore, that these small cyprinids probably play an important role as both a staple and sustaining food for otters in the area. Kruuk *et al.* (1993) argued that otters did not consume small salmonids (<4cm) and Erlinge (1968) stated that small fish were difficult to catch by the otter. However, it is clear from previous studies (Jenkins & Harper, 1980; Wise *et al.*, 1981; Adrian & Delibes, 1987) and from chapter 4 of this thesis that otters do indeed consume significant numbers of small fish. It is possible that the abundance of small cyprinids makes them a more attractive prey than when they are available in small numbers as in Erlinge's experiments.

It is evident therefore, that the distribution of a number of different prey species, and not just salmonids, may have a significant impact on the distribution of otters in riparian environments. In addition, it is also possible that the relationship between otter spraint distribution and physical characteristics of the watercourse or riverbank vegetation may in fact be due to a relationship with prey distribution which will be determined in part by these features of the habitat.

Pollution

A sharp and serious decline in otter populations occurred in England and several other European countries in the mid-1950s, leading to regional extinctions in many areas (Chanin & Jefferies, 1978; Jefferies, 1989). The cause of this decline was undoubtedly the widespread increase in the use of organochlorines in agriculture at about this time. These were shown to have a massive impact on the populations of sparrowhawk *Accipiter nisus* (Newton, 1986), badger *Meles meles* (Jefferies, 1969) and fox *Vulpes vulpes* (Taylor & Blackmore, 1961) among many other species. Many of these species have now recovered from the effects of these pollutants yet otter populations have only recently begun to show evidence of expanding into their former range (Strachan & Jefferies, 1996).

Mason & Macdonald (1993) argued that this may be attributable to the persistence of organochlorine compounds, not only those used in agriculture but also the contamination of British aquatic ecosystems with polychlorinated biphenyl compounds (PCBs) which until recently were widely used in industry. Macdonald & Mason (1988) suggested that PCBs were being used increasingly in the 1950s in addition to the increased use of organochlorines. PCBs were still in use when organochlorines were no longer used in agriculture and it may be this factor that prevented the recovery of otter populations in UK waters. The exact effects of organochlorine and PCB toxicity on otter populations is unknown but there is a substantial amount of evidence to suggest that these compounds may be limiting otter populations at regional scales (Mason 1989, Mason & Macdonald, 1993). However, the situation may be complicated by other factors. For example, Kruuk (1995) argued that in countries with high levels of industrial pollutants there are also significant levels of habitat destruction and reductions in prey populations. In addition the levels of PCBs were relatively high in otters from Shetland which are considered to be a thriving population (Kruuk, Conroy & Carss, 1993). Mason (1993) also showed that levels of PCBs in scats collected in the North Tyne were high yet this is the area of the upper Tyne catchment that produced the highest densities of spraints in the current study (see chapter 3). It is unlikely that PCBs will account for the within-catchment differences in distributions of otter signs observed in this study. In addition

the seasonal fluctuations shown in chapter 3 would be difficult to explain if PCBs were the major determinant of otter distributions.

In addition to organochlorines and PCBs it has been suggested that heavy metal pollution may have effects on otter populations. In particular, Kruuk & Conroy (1991) showed that concentrations of mercury in the tissues of dead otters from Shetland may have been high enough to cause sub-lethal effects. Kruuk *et al.* (1993) showed that mercury levels were higher in Scottish otters from regions where populations were considered to be at risk and lower where populations were apparently thriving. Mason, Last & Macdonald (1986) had concluded ten years ago that heavy metal contamination was not causing direct mortality in British otters. They did, however, find that some individuals contained levels of mercury and lead which approached concentrations known to cause sub-lethal effects. Kruuk *et al.* (1993) showed that levels of cadmium and lead were present in Scottish otter tissues at levels lower than those known to have significant lethal or sub-lethal effects in other mammals. However, the indirect effects of heavy metal pollution on otter populations have not been considered in any of these previous studies. In chapter 2 of this thesis it was noted that their were high levels of zinc, lead and cadmium pollution entering a number of tributaries of the South Tyne as a result of drainage from disused mines in the North Pennines Orefield. Abel & Green (1981) showed that these pollutants had a significant impact on the invertebrate fauna of some of these tributaries. A reduced invertebrate fauna may have had a detrimental impact on the populations of fish in these rivers and consequently on the distribution of otters in the catchment.

In the present study, levels of cadmium, copper, lead and zinc in the tissues of eels caught throughout the upper Tyne catchment were used to investigate the relationship between the distribution of otter signs and heavy metal pollution.

Human disturbance.

Few studies have examined the effects of human disturbance on otter populations and those that did were inconclusive in their findings. The increase in recreational activities on or near watercourses over the last 30 years has been substantial and potential disturbance of the otters' habitat has increased considerably. Macdonald and Mason

(1983) in a study of fifty 5km stretches in Wales used three indices of human disturbance, the numbers of fisherman, population density in parishes and the density of campsites adjacent to the river. None of these were found to be correlated with the density of otter signs. In Shetland where the otter population is thriving (Kruuk, 1995) otters are very tolerant of disturbance. Breeding occurs regularly at Sullom Voe oil terminal and female otters play with cubs in the knowledge that humans are within 10m (pers. obs.)

In freshwater habitats otters are tolerant of a reasonably high level of disturbance provided secure retreats are available during the daytime (Macdonald, 1983). In their radio-tracking survey of otters in Perthshire, Green *et al.* (1984) showed that the male otter often travelled through a town in daylight and swam past fishermen and walkers without being seen. The otter did, however, avoid dogs and reacted adversely to them by quickly leaving the area even if the dogs were unaware of its presence. In some cases otters would not return to the same area for up to three weeks after an encounter with dogs. They also showed that while male otters would remain in resting sites in the presence of people, female otters would immediately abandon an insecure holt site. There is some evidence that sharp and sudden noises cause otters to flee while continuous noises cause little problem (Jefferies, 1987). Otters appear not to avoid urban areas and a number of studies have found otters living in towns (Green & Green, 1980; Macdonald & Mason, 1983). Jefferies (1987) argued that otters were able to tolerate high levels of disturbance as long as sufficient cover was available for them to move about in secrecy. It is possible, however, that females may prefer areas with low levels of disturbance particularly during breeding.

Green *et al.* (1984) and Erlinge (1967a, 1968a) showed that male otters would use a variety of resting sites many of which were above ground and often in disturbed areas. Females however required deep, secure holts in secluded, undisturbed areas, particularly during breeding. It is likely, therefore, that disturbance may have a more significant impact on breeding otters and that lack of secure holts particularly in disturbed areas may restrict breeding. In this chapter a number of indices such as length of footpaths and area of buildings within 100m of the watercourse, were used to determine the potential effects of disturbance on otter populations in the upper Tyne catchment.

5.1.2 The multivariate approach.

Durbin (1993) was unable to find a relationship between otter activity and riverbank vegetation as previously demonstrated by a number of other studies (eg. Mason & Macdonald, 1983). Kruuk (1995) argued that the differences in results were probably due to methodological factors. This may well be the case but not (as Kruuk (1995) believes) because spraint density studies are unreliable but because of differences in the variables studied.

Many studies using spraint density as an indicator of otter habitat utilisation did not consider physical characteristics of the watercourse, though Durbin (1993) did in his work in Deeside. It is possible that riverbank vegetation is correlated with the physical characteristics of a watercourse. Woodland and dense vegetation may be more abundant in those areas with higher fish densities which are often associated with particular river substrata (e.g. Raleigh *et al.*, 1986). Kruuk *et al.* (1993) compared otter activity with stream width and demonstrated a relationship which they argued was the result of higher densities of salmonids in small streams. They did not, however, consider the effects of other features of the habitat in their study.

There are no previous studies (spraint density or telemetry based) which have considered the relationship between otter distribution and both habitat and prey availability variables in the same statistical analysis. In chapter 3 it was shown that the number of otter signs in the upper Tyne catchment was low and that patterns in spraint distribution were best described as presence or absence per unit sampling stretch. In this chapter logistic regression (Tabachnick & Fidell, 1996) is used to model predictively the presence or absence of otter signs in the upper Tyne catchment using a number of environmental parameters including riverbank vegetation, physical characteristics of the watercourse, prey availability and heavy metal pollution.

Logistic regression has been used in a number of studies to model the distribution of vertebrate species. For example Osborne & Tigar (1992) used logistic models to predict the probabilities of occurrence of bird species in Lesotho and Buckland & Elston (1993)

used similar methods to model deer census data. However, all previous studies have ignored the spatial arrangement of the data. It was shown in chapter 3 that the distribution of otter signs in the upper Tyne catchment was clumped and exhibited a high degree of spatial autocorrelation. It was argued that this was caused by either underlying environmental factors which were also spatially autocorrelated (reactive effects) or by the influence of one location on its neighbours as a result of otter behaviour (interactive effects). If all the environmental factors responsible for the spatial distribution are not included in the model and/or there is a significant interactive component to the distribution of otter signs, the spatial pattern of otter signs will not be explained fully by the measured variables. However, by incorporating an additional covariate into the model that is a measure of the spatial autocorrelation in the data it is possible to quantify how much of the spatial distribution is not explained. In this chapter an autologistic approach which takes account of the spatial autocorrelation in the dataset (Smith, 1994; Augustin *et al.*, 1996) is used to model the distribution of otter signs.

5.2 METHODS

5.2.1 Physical features of the watercourse.

Width, depth and substrate type.

Width, depth and substrate type were assessed at 100m intervals (measured by pacing) for each 5km stretch. The width at each 100m interval was estimated visually and classified into one of the following width categories;

WID1:	≤5m
WID2:	>5≤10m
WID3:	>10≤20m
WID4:	>20≤30m
WID5:	>30m

Depth was determined by wading as near to the centre of the watercourse as possible and measuring using a pole marked into the following categories;

DEP1:	≤0.1m
DEP2:	>0.1≤0.25m
DEP3:	>0.25≤0.5m
DEP4:	>0.5≤1m
DEP5:	>1≤1.5m
DEP6:	>1.5m

Width and depth were recorded in each of the four seasonal surveys.

The riverbed substrate type was recorded at each 100m interval by wading as near to the centre of the watercourse as possible and classifying into the following categories;

SUB1:	Sand/silt
SUB2:	Gravel (stones less than 10cm in diameter)
SUB3:	Gravel/cobble (stones up to 20cm in diameter)
SUB4:	Cobble (stones >10≤20cm in diameter)
SUB5:	Large rocks/boulders/bedrock

Substrate type was not recorded for the three 5km stretches around the shores of Kielder reservoir.

For each 5km and 2.5km stretch the total number of 100m sections in each width, depth and substrate category were recorded in an Excel spreadsheet.

The width, depth and substrate categories containing the median or modal number of 100m sections were calculated for each 1km stretch while at the 600m and 200m sample unit sizes the width, depth and substrate category was determined from the 100m section containing the stretch centroid (see chapter 3).

Altitude

The altitude for each survey stretch was determined by overlaying a point coverage containing the locations of the stretch centroids (using the Dynamic Segmentation command EVENTPOINT to convert the centroid measures contained in an event table to a point coverage) over a digital terrain model of the catchment. The TINSPOT command was then used to determine the altitude at these centroid locations. The altitude variable ALT was added to the event table of centroid measures which could then be transferred to an Excel spreadsheet as an ASCII text file for further analysis. This process was carried out for each of the sample unit sizes.

5.2.2 Riverbank vegetation

During each of the four seasonal surveys riverbank vegetation within 5m of the water's edge was recorded onto 1:10000 Ordnance Survey maps into one of the following categories

VEG1	No vegetation and close-mown or heavily grazed ground.
VEG2	Vegetation up to 10cm in height.
VEG3	Vegetation greater than 10cm but less than 1m in height.
VEG4	Herbaceous vegetation greater than 1m in height.
VEG5	Open canopy woodland - defined as woodland with the edges of individual tree canopies at least 2m apart.
VEG6	Closed canopy woodland - defined as woodland with the edges of individual tree canopies touching or overlapping.

The start and end points of each habitat section were recorded onto the 1:10000 Ordnance Survey maps. The locations of each start and end point were then digitised into the GIS and automatically converted into start and end measures in a Dynamic Segmentation event table using Arc/Info routines. The resultant event tables were then overlaid onto the route systems for the 5km, 2.5km, 1km and 600m survey stretches created in chapter 4. The database table produced from these overlays were then transferred to Microsoft Excel spreadsheets and the total length of each habitat type calculated for the 5km and 2.5km sample unit sizes. For 1km and 600m sample unit sizes the habitat type which covered the highest proportion of riverbank was calculated for each stretch. At the 200m sample unit size the habitat type at the centroid location only was recorded by overlaying the centroid event table with the habitat event table.

5.2.3 Availability of potential holts

During the four surveys the location and description of all potential holt sites (HOLTS) was marked on the 1:10000 maps. Potential holts were considered to be any holes in the riverbank which were large enough and deep enough to allow entry to otters and remain dry for most of the year. These also included large stable areas of flood debris which had built up over a long time period. It should be emphasised that, in many cases, holts that are being used by otters do not show any physical evidence of this usage (Kruuk, 1995) and individual otters will often rest in the open without the need for secure sites (Green *et al.* 1984). However, the availability of potential holt sites was considered to be a reasonable indicator of the "quality" of stretches in terms of provision of shelter for otters.

The co-ordinates of each holt location were used to create a point coverage of holt sites using the ARC GENERATE command. This was converted to a Dynamic Segmentation event table of measure values for each holt along the route system, for each stretch of riverbank. This was then used to determine the total number of holts in each 5km, 2.5km and 1km stretch. At the 600m and 200m sample unit sizes the presence or absence of holt sites only was recorded.

5.2.4 Prey availability

Prey populations were determined through electro-fishing at a number of sites throughout the upper Tyne catchment as described in chapter 4. It was shown in that chapter that accurate population estimates could be obtained for only some of the species encountered during the electro-fishing programme. In addition, it was shown that certain size classes of fish were important in the otters' diet. Therefore, the following variables were used in this chapter in assessing the relationship between presence of otter signs and the distribution of prey species;

SMTOT	presence or absence of salmon.
TRLT90	presence or absence of trout >80≤90mm in length.

TRTOT	Density (Number of fish per $100m^2$) of all trout.
SALLT90	Density (Number of fish per $100m^2$) of salmonids >80≤90mm in length.
SALTOT	Density (Number of fish per $100m^2$) of all salmonids.
SLTOT	Density (Number of fish per $100m^2$) of all stoneloach.
EELTOT	Presence or absence of eels.
MINTOT	Presence or absence of minnow.

The co-ordinates of each electro-fishing site were converted into a GIS point coverage using the ARC GENERATE command. This was then used to create a Dynamic Segmentation event table containing the measure values for each electro-fishing site based on the 5km route-system.

At the 5km sample unit size electro-fishing sites which occurred within the same 5km stretch were pooled to provide a density estimate of each fish species for each 5km stretch (or presence or absence of each species where appropriate). At the 2.5km and 1km sample unit sizes electro-fishing sites were assigned to those stretches which contained their measure value to give estimates of fish populations at these unit sizes. At the 600m and 200m sample unit sizes electro-fishing sites were assigned to those stretches which contained their measure value or were within 100m of this. Since only 97 sites were electro-fished not all sample units contained an electro-fishing site. This led to a reduction in sample sizes in subsequent analyses. Table 5.2.1 gives the number of stretches at each sample unit size. The distribution of prey determined from this survey was compared with the distribution of otter signs in the summer only since extrapolation of prey estimates to other seasons would be invalid. The validity of using small numbers of electro-fishing sites as representative of the fish populations in stretches of river at the various sample unit sizes is discussed in section 5.4.

Table 5.2.1 Number of stretches of riverbank surveyed for otter signs containing electro-fishing sites during a survey of prey populations in the upper Tyne catchment during the summer of 1995.

Sample unit size	Number of stretches
5km	35
2.5km	59
1km	83
600m	79
200m	72

5.2.5 Heavy metal pollution

During the 1995 electro-fishing survey a single eel was taken from fifty sites in the upper Tyne catchment for heavy metal analysis (Figure 5.2.1). Each eel was anaesthetised, measured and then killed using a concentrated dose of anaesthetic (MS222). All eels were then frozen prior to analysis.

Approximately 4g of skinned muscle tissue was dissected from behind the anus giving an approximate dry weight of 1g of tissue. Whole livers were removed and dried. These were then placed in concentrated nitric acid for a period of three days at room temperature and then refluxed for 12-24 hours. The nitric acid was evaporated until the material was just dry and then dissolved in exactly 5ml 3N hydrochloric acid. This was filtered and concentrations of cadmium (Cd), copper (Cu), lead (Pb) and zinc (Zn) determined by atomic absorption spectrophotometry. The spectrophotometer was calibrated with standard solutions covering the following ranges: Cd 0.2-1.0ppm; Cu, Pb and Zn 1.0-5.0ppm. All metal concentrations were expressed as μg/g of tissue. Laboratory analysis was carried out by Tom Mercer under the direction of Professor Evans at the University of Durham. The work was carried out under separate contract to the National Rivers Authority - Northumbria Region.

5.2.6 Human disturbance

To assess the potential effects of human disturbance the following eight variables were chosen as possible indicators;

AROAD	total length of A-roads within a 100m buffer of the survey stretch.
BROAD	total length of B-roads within a 100m buffer of the survey stretch.
PATH	total length of footpaths and bridleways within a 100m buffer of the survey stretch.
BUILD	total area of buildings within 100m buffer of the survey stretch.
CAMP	presence or absence of campsites within a 100m buffer of the survey stretch.
PICNIC	presence or absence of picnic sites within a 100m buffer of the survey stretch.
CARPARK	presence or absence of car parks within a 100m buffer of the survey stretch.

AROAD, BROAD, PATH and BUILD were determined by converting the Dynamic Segmentation route system at the 5km, 2.5km, 1km and 600m scales into line coverages using the EVENTARC command. At the 200m sample unit size the centroid event table was used to create a point coverage of centroid locations for each stretch. A 100m buffer was then created around each survey stretch for the larger sample unit sizes. The buffer was flat-ended so that there was no overlap between neighbouring buffers. At the 200m sample unit size a 90m buffer was created since this was the maximum distance at which neighbouring circular buffers did not overlap. The resultant buffer polygon coverages were overlaid using the IDENTITY command onto the AROADS, BROADS, PATHS, BUILDS, CAMPSITE, PICNIC and CARPARK coverages created in chapter 3. The resultant database tables were then transferred to an Excel spreadsheet where the values of the variables described above were calculated for each sample unit.

5.2.7 Statistical analysis

Exploratory data analysis.

Variables which are dichotomous, categorical or continuous can be used in logistic regression analysis. For continuous variables, assumptions regarding the distributions of predictor variables are not required. However, multivariate normality and linearity among predictors may enhance the power of resultant logistic models (Tabachnick & Fidell, 1996). In addition, frequency distributions must be truly continuous and not multimodal. Therefore, frequency distributions for all continuous variables were tested for normality using Kolmogorov-Smirnov goodness of fit tests. Any variables which were non-normally distributed were investigated for outliers and then transformed to normality. Those variables that were not normally distributed were examined further and in most cases found to be multi-modal and were therefore converted to categorical variables. Categorical variables were used in statistical analyses after first being converted to a series of dichotomous dummy variables (e.g., the depth variable was converted to presence or absence of DEP1; presence or absence of DEP2, presence or absence of DEP3 and so on).

Removing redundant variables

Logistic regression is sensitive to extremely high correlations among predictor variables signified by very high standard errors for parameter coefficients. In addition too few cases relative to the number of predictor variables may result in the failure of logistic models due to overfitting (Tabachnick & Fidell, 1996). To overcome these problems Pearson product-moment correlations were calculated between all pairs of variables. For each group of variables that were significantly correlated only the one with the highest correlation coefficient was kept for subsequent analysis. If two variables had the same correlation coefficients the most biologically meaningful variable was retained.

Accounting for spatial autocorrelation

Some of the spatial autocorrelation in the distribution of otter signs will be explained by some of the predictor variables included in the logistic regression models. However, as argued in the introduction this will not necessarily account for all the spatial autocorrelation in the distribution of otter signs. To overcome this, additional covariates (spatial autocovariates) were added to the model which take account of the spatial distribution of the presence of otter signs. These covariates were created to account for autocorrelation at given distances between sample units. They were determined using a set of distance filters derived from the spatial autocorrelation analyses carried out in chapter 3. The filters used at each sample unit size are given in Table 5.2.2.

Table 5.2.2 Distance filters used in determining logistic regression autocovariates describing the spatial distribution of otter signs in the upper Tyne catchment in between 1993 and 1994.

Sample unit size	Season	Autocovariate	distance filter (km)
5km	Spring	None	-
	Summer	LAG1	≥20<30
	Autumn & Winter	LAG1	>10≤20
2.5km	All	LAG1	≥2≤3
	All	LAG2	≥10<30
	Autumn	LAG3	>30
1km	All	LAG1	≥1≤5
	All	LAG2	≥10≤40
	All	LAG3	>50
600m	All	LAG1	≥0.6≤5
	All	LAG2	≥10≤30
	All	LAG3	>30≤100
200m	All	LAG1	≥0.2≤5
	All	LAG2	≥10≤30
	All	LAG3	>30≤100

The spatial autocovariate for each sample stretch *i* was calculated as the proportion of neighbouring (at a specified distance filter) sample stretches with otter signs present.

These spatial autocovariates were calculated for datasets containing all sample locations at each sample unit size and for those containing only electro-fishing sample sites and those with heavy metal data. The calculations of distance filters and determination of spatial autocovariates were carried out in SPACESTAT.

Autologistic regression modelling

The variables remaining after correlation analysis (excluding spatial autocovariates) were used in subsequent analyses. Logistic regression at all sample unit sizes was first conducted using the physical characteristics, riverbank vegetation, potential holt site and disturbance variables for which the largest number of cases were available. The variables that were retained in these models were then used in conjunction with the prey availability data (summer only) or heavy metals (after reducing the number of prey variables in the summer) for which a reduced number of cases were available. The effect of this was to reduce problems due to low cases-to-variables ratios by reducing the number of variables in the analysis at the smaller sample sizes.

All logistic regression modelling was conducted in SPSS for Windows (Norusis, 1993c) using a forward stepwise technique to select those variables that contributed the most to group (presence or absence) separation with inclusion of variables based on the significance of the log-likelihood ratio (Tabachnick & Fidell, 1996). To overcome the problem of important predictors being excluded from the logistic model due to displacement by another predictor or combination of predictors, variables were included with a log-likelihood significance of <0.18. This was within the range recommended by Hosmer & Lemeshow (1989) to ensure entry of variables with coefficients different from zero.

Two subsets (75% and 25% of samples) were chosen at random from the overall sample. Stepwise logistic regression was performed on the larger subset. This was repeated 25 times and those variables that were selected in more than 50% of the 25 iterations were used to build the final logistic model. To validate this final model 10 new random

subsets of 75% and 25% of the overall sample were created. Logistic regression was run on the larger subset and the resultant model used to classify cases in the smaller subset. The frequencies of correct classifications in each of the 10 iterations were then recorded to produce estimates of the ability of the model to correctly classify cases in the smaller subset (cross-validation). To estimate how the final model performed, the mean correct classification rate (calculated from the 10 iterations) for stretches with and without otter signs was compared with that attainable by chance using Cohen's kappa, the significance of which was tested using a z-test (Weidemann & Fenster, 1978).

The stability of the sub-sampling procedure was determined by comparing the mean coefficient calculated for each variable from the 10 iterations with the coefficient calculated from the full model using 100% of cases.

To account for spatial autocorrelation in the distribution of otter signs the spatial autocovariates were added to the logistic models resulting from the above procedures. If the spatial autocovariates added significantly to the logistic models these were then tested using the split-sample validation procedure outlined above. The spatial autocovariates were re-calculated for both the 75% and 25% parts of the sample in each iteration of this procedure since splitting the sample removed the spatial relationship between some sample units and their neighbours. To determine whether these models performed better than those without the spatial autocovariate, the mean correct classification rates for both models were compared. If no difference was found then spatial autocorrelation was not considered to be a factor in predicting the presence or absence of otter signs. If a difference was found between the two models then the environmental variables in the logistic models were not accounting for all of the spatial pattern in the distribution of otter signs.

Comparing North Tyne with South Tyne

It was shown in chapter 3 that the proportion of stretches with otter signs was significantly higher in the North Tyne than in the South Tyne in the Summer and Autumn at the 1km, 600m and 200m sample unit sizes. Therefore, to determine which environmental variables may have been responsible for this difference, new dichotomous variables were created at each sample unit size which defined each stretch as either South

Tyne (given the value of 1) or North Tyne (given the value of 2). These new variables were then used in logistic regression models to predict group membership (i.e. North or South Tyne) from environmental variables on the assumption that North Tyne stretches contained more otter signs than South Tyne stretches. Significant correlations between predictor variables, the catchment variable and other predictor variables were first determined from a matrix of Pearson product-moment correlation coefficients. As outlined above, for each group of variables that were significantly correlated only one was kept for subsequent analysis. These were then used in logistic regression models using the same procedures as outlined previously.

5.3 RESULTS

5. 3. 1 Predicting presence or absence in sampling units.

Exploratory data analysis

Depth

There were very few 100m sections in depth class DEP4 (>1m) in any of the 5km stretches of river in any season. Therefore, this category was combined with depth class DEP3 (>0.5≤1m) to create a new DEP3 of >0.5m. The frequency distributions for each depth class were transformed to provide an approximation to a normal distribution (confirmed with Kolmogorov-Smirnov goodness-of-fit tests). At the 2.5km sample unit size the frequency distributions of the number of 100m sections per 2.5km stretch in each depth class were not continuous but were better described as a single categorical variable with each 2.5km stretch assigned to one of the following categories if the median number of 100m sections fell within that class;

DEP1	≤0.25m
DEP2	>0.25≤0.5m
DEP3	>0.5≤1m
DEP4	>1m

At the 1km and 600m sample unit sizes depth was described by categorical variables as outlined in section 5.2. At the 200m sample unit size there were few stretches in depth class DEP2 therefore this was combined with DEP1 to give a new depth class of ≤ 0.5m. Tables VIII.Ia to VIII.Ie in Appendix VIII give summary statistics for all depth classes at all sample unit sizes for total samples and separated into North and South Tynes and presence or absence of otter signs.

Width

The frequency distributions of the number of 100m sections of riverbank in each width class were not normally distributed at the 5km sample unit size (even after transformation). Examination of the frequency distributions showed that due to the small sample size there were two distinct width classes in all seasons - ≤10m and >10m. Therefore a single dichotomous variable was created where 0 was assigned to any 5km stretch with a median number of 100m sections in width classes ≤10m (WID1 and WID2) and 1 assigned to any stretches in width classes >10m (WID3, WID4 and WID5). Examination of frequency distributions at the 2.5km sample unit size showed that there were few stretches in width classes WID3 (>10≤20m) and WID4 (>20≤30m) depending on the season. Therefore these two classes were combined to give a new set of width categories;

WID1	≤5m
WID2	>5≤10m
WID3	>10≤30m
WID4	>30m.

At the 1km, 600m and 200m sample unit sizes river width was described by the methods outlined in section 5.2. Tables VIII.IIa to VIII.IIe in Appendix VIII give summary statistics for all width classes at all sample unit sizes for total samples and separated into North and South Tynes and presence or absence of otter signs.

Substrate

Very few 100m sections in substrate class SUB1 (sand/silt) were recorded for any of the 5km stretches surveyed and at other sample unit sizes no sample stretches were described by this substrate class. Therefore, this substrate category was ignored in subsequent analyses. The revised substrate classes used were defined as follows;

SUB1: gravel
SUB2: gravel/cobble
SUB3: cobble
SUB4: boulders and bedrock

At the 5km sample unit size the frequencies of the number of 100m sections per 5km stretch in each substrate class were log-transformed to approximate normal distributions. Tables VIII.IIIa to VIII.IIIe in Appendix VIII gives summary statistics for all substrate classes at all sample unit sizes for total samples and separated into North and South Tynes and presence or absence of otter signs.

Altitude

At the 5km sample unit size the altitude at each centroid location was transformed to ensure that the frequency distribution was approximately normal. At the 2.5km sample unit size the altitude frequency distribution was not continuous but comprised of two modes with peaks at 188m and 250m. Therefore, a single dichotomous variable was created with 0 assigned to stretches with altitudes of >100≤200m and 1 to stretches with altitudes of >200m. The altitude frequency distribution at the 1km scale consisted of four modes with peaks at 125m, 188m, 250m and 375m. Therefore each stretch of riverbank was assigned to one of the following altitude classes;

ALT1	>50≤150m
ALT2	>150≤225m
ALT3	>225≤300m
ALT4	>300m

At the 600m and 200m sample unit sizes the frequency distributions had an additional fifth mode with a peak at 500m so the following five altitude classes were used at this scale. Tables VIII.IVa to VIII.IVe in Appendix VIII give summary statistics for all altitude classes at all sample unit sizes for total samples and separated into North and South Tynes and presence or absence of otter signs.

Potential holt sites

Table 5.3.1 shows the proportions of potential holts of different types found during the four surveys of the upper Tyne catchment. The majority were found in the roots of large bank-side trees with the remainder occurring in rocky crevices or man-made structures and substantial piles of riverbank flood debris.

Table 5.3.1 Number and proportions of potential holt sites of different types found during four surveys of forty 5km stretches of riverbank in the upper Tyne catchment between March 1993 and November 1994.

Type of holt	Number	Proportion (%)
Rocky bank, gabion,caves ,etc.	71	33
Sycamore	38	18
Ash	29	14
Elm	12	6
Oak	11	5
Alder	9	4
Beech	9	4
Birch	8	4
Hazel	3	1
Willow	2	1
Scots Pine	1	0.5
TOTAL TREES	122	58
Debris piles/holes in bank	19	9

The total number of potential holts per 5km stretch is given in Table 5.3.2. There was a high proportion of 5km stretches without holts (30%) and of the stretches with holts only seven produced more than 10 potential sites. Therefore, it was decided to reclassify the number of potential holts as a single dichotomous variable of presence or absence of potential holt sites as for the other sample unit sizes. Table VIII.V in Appendix VIII shows the percentages of stretches of riverbank with potential holts present at all sample

unit sizes. Results are given for the overall sample, for North and South Tyne separately and for stretches with or without otter signs during four surveys in different seasons.

Table 5.3.2 The number of potential holt sites found in each 5km stretch of riverbank in the upper Tyne catchment during four surveys between 1993 and 1994.

5km stretch code	Number of potential holts	5km stretch code	Number of potential holts
1	22	21	4
2	14	22	0
3	0	23	0
4	7	24	0
5	9	25	0
6	1	26	8
7	20	27	3
8	15	28	0
9	3	29	8
10	9	30	1
11	0	31	0
12	7	32	3
13	7	33	2
14	1	34	0
15	2	35	1
16	1	36	0
17	7	37	18
18	13	38	15
19	4	39	0
20	7	40	0

Riverbank vegetation

The frequencies of the total length of each vegetation type in each 5km stretch were not normally distributed even after transformation. Examination of frequency distribution histograms showed that they were non-continuous probably due to the small sample size at this scale. Therefore, a single dichotomous variable was created with 1 assigned to wooded (VEG4 + VEG5 + VEG6) and 0 to non-wooded (VEG1 + VEG2 + VEG3) stretches.

At the 2.5km sample unit size there were few stretches assigned to VEG1 (bare ground) in all seasons except winter therefore these were combined with VEG2 (low vegetation). In addition, there were few stretches assigned to VEG3 (dense vegetation and shrubs) and these were therefore combined with VEG4. Consequently, for Spring, Summer and Autumn the following new vegetation categories were used in subsequent analyses;

VEG1: bare ground plus vegetation less than 0.1m in height
VEG2: vegetation >0.1<1m in height.
VEG3: vegetation >1m, shrubs and open canopy woodland
VEG4: closed canopy woodland.

For the Winter sample five vegetation categories were used;

VEG1: bare ground
VEG2: vegetation <0.1m in height
VEG3: vegetation >0.1<1m in height.
VEG4: vegetation >1m, shrubs and open canopy woodland
VEG5: closed canopy woodland.

At the 1km and 600m sample unit sizes the vegetation categories as outlined in section 5.2 were used while at the 200m sample unit size the same categories as the 2.5km scale Spring, Summer and Autumn samples were used. Tables VIII.VIa to VIII.VIe in

Appendix VIII give summary statistics for all riverbank vegetation classes at all sample unit sizes for total samples and separated into North and South Tynes and presence or absence of otter signs.

Prey availability

The frequency distributions for the densities of all salmonids, all trout and stoneloach at the 5km sample unit size were not continuous. Therefore, new categorical variables were created as follows. For salmonids and trout three density classes were used; ≤15 fish, >15≤50 fish and >50 fish. For stoneloach three density classes were also recognised; no fish, >0≤25 fish, >25 fish.

At all other sample unit sizes the densities of salmonids and trout in the sample were normally distributed after transformation while stoneloach was categorised into the three density classes outlined above. Tables VIII.VIIa to VIII.VIIi in Appendix VIII give summary statistics for all fish density classes at all sample unit sizes for total samples and separated into North and South Tynes and presence or absence of otter signs.

Heavy metals

Kolmogorov-Smirnov goodness-of-fit tests showed that the frequency distributions of all heavy metal concentrations in both types of eel tissues were non-normal. The results of analyses for lead and copper in muscle tissue revealed two outliers in the sample. These were truncated to values 0.05 and 0.1 higher than the next smallest values to reduce their influence on the frequency distributions. After transformation all frequency distributions were then approximately normal. Table 5.3.3 shows that none of the metal concentrations were correlated with eel length so no corrections for this were used. Table VIII.VIIIa in Appendix VIII gives the mean concentrations (in μg/g of tissue) of each heavy metal for both muscle and liver for the whole sample and the North and South Tyne separately. Tables VIII.VIIIb to VIII.VIIId give the mean concentrations (in μg/g of tissue) of each heavy metal for both tissue types for stretches of riverbank with or without otter signs at four sample unit sizes. Results are not presented for the 200m

sample unit size because the numbers of stretches with otter signs which also had data on heavy metal concentrations were too small to enable comparisons.

Table 5.3.3 Coefficients of linear correlation between fish length and heavy metal concentrations (in μg/g) in muscle and liver tissue of fifty eels captured during an electro-fishing survey of the upper Tyne catchment in the summer of 1995. NS denotes not significant.

Heavy metal	Tissue	Correlation with fish length coefficients
Cadmium	Muscle	-0.25^{NS}
	Liver	-0.25^{NS}
Copper	Muscle	-0.07^{NS}
	Liver	0.06^{NS}
Lead	Muscle	-0.02^{NS}
	Liver	-0.01^{NS}
Zinc	Muscle	-0.05^{NS}
	Liver	-0.01^{NS}

Human disturbance indices

At all sample unit sizes there were only short lengths of A-road within 100m buffers of the riverbank and many stretches did not contain any A-roads within this buffer. Therefore, this variable was reclassified as a single dichotomous variable of presence or absence of A-roads. At the 5km sample unit size the frequency distribution of lengths of B-roads within the 100m buffers was not continuous and was reclassified as a variable with three categories based on the following lengths of road;

BROAD1	<50m
BROAD2	≥50<250m
BROAD3	>250m

Similarly the frequency distributions of lengths of footpath and bridleway within the 100m buffers were also non-continuous and were converted into categorical variables based on the following length classes;

PATHS1	<50m
PATHS2	≥50<200m
PATHS3	>200m

The frequency distributions of the total area of buildings within the 100m buffers were not continuous at the 5km sample unit size and were reclassified as variables with three categories based on the following areas;

BUILD1	<500m^2
BUILD2	≥500<1500m^2
BUILD3	>1500m^2

At all other sample unit sizes the total length of B-roads within the 100m buffer was reclassified as a single dichotomous variable of presence or absence of B-roads. The total length of paths within the 100m buffer at the 2.5km and 1km sample unit sizes were categorised using the following classes;

PATHS1	≤50m
PATHS2	>50≤150m
PATHS3	>150≤500m
PATHS4	>500m

The total area of buildings within the 100m buffer at these sample unit sizes were categorised using the following four classes;

BUILD1	No buildings
BUILD2	>0≤1000m^2
BUILD3	>1000≤3000m^2
BUILD4	>3000m^2

At the 600m and 200m sample unit sizes there were high numbers of stretches without any of the variables described above. Therefore at these sample unit sizes all disturbance variables were re-classified as being present or absent within the buffer area. Tables VIII.IXa to VIII.IXj in Appendix VIII give summary statistics for all disturbance variable classes at all sample unit sizes for total samples and separated into North and South Tynes and presence or absence of otter signs.

Variables correlated with presence or absence of otter signs

Tables 5.3.4 to 5.3.8 show those variables that were correlated with the presence or absence of otter signs which have a component of their coefficients which is not explained by their correlation with any other predictor variables at each of the five sample unit sizes.

Table 5.3.4 Significant Pearson product-moment correlation coefficients between the presence or absence of otter signs in 5km stretches of riverbank in four surveys between 1993 and 1994 and those environmental variables which have a component of their correlation coefficient which is not explained by any other variables. * denotes significant at $p < 0.05$; ** denotes significant at $p < 0.01$. ALTITUDE and SUB3 were log-transformed before analysis.

Variable	n	Spring	Summer	Autumn	Winter
ALTITUDE (m)	40	-	-0.59**	-0.53**	-0.53**
VEGETATION (wooded or non-wooded)	40	-	0.57**	0.53*	-
SUB3 (cobble only)	40	0.41**	-	-	-
WIDTH (≤10m or >10m)	40	0.41**	-	-	-
BUILD1 (<500m^2)	40	-	-0.32*	-	-
SALMON (presence or absence)	33	No data	0.53*	No data	No data

Table 5.3.5 Significant Pearson product-moment correlation coefficients between the presence or absence of otter signs in 2.5km stretches of riverbank in four surveys between 1993 and 1994 and those environmental variables which have a component of their correlation coefficient which is not explained by any other variables. * denotes significant at $p < 0.05$; ** denotes significant at $p < 0.01$. ALTITUDE and SUB3 were log-transformed before analysis.

Variable	n	Spring	Summer	Autumn	Winter
ALTITUDE (m)	70	-0.40**	-0.43**	-0.45**	-0.52**
DEP3 (>0.5≤1m)	70	-	-	0.37**	-
WID1 (≤5m)	70	-0.35**	-	-	-
WID3 (>10≤30m)	70	-	-	-	0.25*
WID4 (>30m)	70	-	-	0.33**	-
HOLTS (presence or absence)	70	0.43**	0.29*	0.29*	-
VEG1 - bare ground and low vegetation (bare ground only in winter)	70	-0.38**	-	-0.27*	-0.34**
VEG4 (Spring, Summer & Autumn) & VEG5 (Winter) - closed canopy woodland	70	-	0.41**	0.39**	-
BUILD4 (>3000m^2)	70	-	0.34**	-	-
LOACH1 (no stoneloach)	59	No data	-0.43**	No data	No data
EEL (presence or absence)	59	No data	0.28*	No data	No data
Liver Cadmium (μg/g)	33	-	0.39*	-	-
LAG1	70	0.43**	0.67**	0.70**	0.59**

Table 5.3.6 Significant Pearson product-moment correlation coefficients between the presence or absence of otter signs in 1km stretches of riverbank in four surveys between 1993 and 1994 and those environmental variables which have a component of their correlation coefficient which is not explained by any other variables. * denotes significant at $p < 0.05$; ** denotes significant at $p < 0.01$. Liver Lead concentrations were log-transformed before analysis.

Variable	n	Spring	Summer	Autumn	Winter
ALT1 (>50≤150m)	182	0.18*	0.30**	0.39**	-
ALT2 (>150≤225m)	182	-	0.27**	-	-
DEP3 (>0.5≤1m)	182	-	-	0.37**	-
WID4 (>20≤30m)	182	0.17*	-	-	0.32**
WID5 (>30m)	182	-	0.21	-	-
HOLTS (presence or absence)	182	-	0.19*	0.19**	0.28**
VEG2 - low vegetation	182	-0.24**	-	-	-
VEG3 - vegetation >0.1≤1m	182	-0.19**	-	-0.37**	-0.24**
PATHS2 (>0≤150m)	182	-0.16*	-	-	-
MIN (presence or absence)	83	No data	0.51**	No data	No data
Muscle Cadmium (μg/g)	45	-	-	0.33**	-
LAG1	182	0.33**	0.79**	0.67**	0.70**

Table 5.3.7 Significant Pearson product-moment correlation coefficients between the presence or absence of otter signs in 600m stretches of riverbank in four surveys between 1993 and 1994 and those environmental variables which have a component of their correlation coefficient which is not explained by any other variables. Muscle Zinc concentrations were log-transformed before analysis. * denotes significant at $p < 0.05$; ** denotes significant at $p < 0.01$.

Variable	n	Spring	Summer	Autumn	Winter
ALT1 (>50≤150m)	304	0.23**	0.28**	0.27**	0.22**
ALT5 (>400m)	304	-	-	-	-0.18**
DEP3 (>0.5≤1m)	304	-	-	0.21**	-
WID1 (≤5m)	304	-0.25**	-	-	-
WID2 (>5≤10m)	304	-	-	-	-0.22**
SUB3 (gravel/cobble)	304	-	-	-	0.14*
HOLTS (presence or absence)	304	0.41**	0.24**	0.23**	0.26**
VEG2 (up to 10cm in height)	304	-0.17**	-	-	-
VEG5 (open canopy woodland)	304	-	0.19**	-	-
VEG6 (closed canopy woodland)	304	-	-	0.16**	0.18**
LOACH2 (presence or absence of >0≤25 fish $100m^{-2}$)	79	No data	0.35**	No data	No data
MIN (presence or absence)	79	No data	0.51**	No data	No data
LAG1	304	0.49**	0.72**	0.51**	0.56**

Table 5.3.8 Significant Pearson product-moment correlation coefficients between the presence or absence of otter signs in 200m stretches of riverbank in four surveys between 1993 and 1994 and those environmental variables which have a component of their correlation coefficient which is not explained by any other variables. * denotes significant at $p < 0.05$; ** denotes significant at $p < 0.01$

Variable	n	Spring	Summer	Autumn	Winter
ALT1 (>50≤150m)	498	-	0.16**	-	-0.20**
WID1 (≤5m)	498	-0.20**	-	-	-
SUB4 (boulders and bedrock)	498	-	0.13**	0.14**	-
HOLTS (presence or absence)	498	0.28**	-	0.16**	-
VEG5 (open canopy woodland)	498	-	0.14**	-	-
VEG6 (closed canopy woodland)	498	-	0.20**	0.14**	-
MIN (presence or absence)	72	No data	0.33**	No data	No data
LAG1	498	0.45**	0.48**	0.39**	0.52**

Autologistic regression models.

Tables 5.3.9 to 5.3.13 show the resultant logistic regression models for the each sample unit size in each season using the variables outlined in Tables 5.3.4 to 5.3.8. For each model the results of the cross-validation procedure are given. The logistic models containing the spatial autocovariate are also given. The mean coefficients for each variable calculated from the 10 iterations of the cross-validation differed from the coefficients in the full model by less than 10% in all runs at all sample unit sizes. This suggested that all of the predictor variables were stable in the resultant.

At the 5km sample unit size the logistic regression models predicted the presence or absence of otter signs significantly better than chance in the autumn only. Otter signs were found in wooded stretches at low altitude (Table 5.3.9).

At the 2.5km sample unit size the logistic regression model for Spring predicted the presence or absence of otters significantly better than chance (Table 5.3.10). Otter signs were more likely to be present in this season in 2.5km stretches at altitudes of less than 200m which contain holt sites and are vegetated. The spatial autocovariate did not add to the predictive power of the model in the Spring. In the Winter the presence or absence of otter signs was also predicted significantly by the logistic regression model with otter signs more likely to be present at altitudes of less than 200m. The addition of the spatial autocovariate did not significantly improve the model.

At the 1km sample unit size the presence or absence of otter signs was predicted by the environmental variables in the summer only (Table 5.3.11). The presence of minnows and low altitudes were the best predictors of the presence of otter signs. In the winter the presence or absence of otter signs could be predicted only when the spatial autocovariate was included in the model.

At the 600m sample unit size the presence or absence of otter signs in the spring was predicted by the logistic regression model (Table 5.3.12). Stretches wider than 5m at low altitude containing holt sites more likely to contain otter signs in this season. The addition of the spatial autocovariate slightly improved the model. In the summer the presence or absence of otter signs was correctly predicted by the presence of minnows

and stoneloach and the distribution of woodland. The addition of the autocovariate only slightly improved the model.

At the 200m sample unit size all logistic models failed to predict the presence or absence of otters except in the summer and summer and autumn when the spatial autocovariate was added. In the Spring the constant only remained in the logistic regression model. Therefore, no further analysis was carried out in this season.

Table 5.3.9 Logistic regression models predicting the presence or absence of otter signs in 5km stretches of river from habitat variables in four surveys of the upper Tyne catchment between 1993 and 1995. B and SE (B) are the regression coefficients and standard errors for each variable, R is a measure of the partial correlation between the variable and the presence or absence of otter signs after all the other variables have been taken into account. The ability of the models to predict presence or absence of otter signs was tested by comparing the mean percentage of correct classifications in a 10 iteration cross-validation procedure with that expected if the models were predicting at random using Cohen's kappa.

SPRING (LARGE SAMPLE)

Variable	Transformation	B	SE (B)	R	Mean percentage correct classifications (%)		
SUB3 (cobble)	$Log_{10}(x + 1)$	2.87	1.08	0.30	Absent	Present	Overall
WID (≤10 or >10m)	-	2.97	1.11	0.32	73.6	61.7	68.0
Constant	-	-3.02	1.15		k = 0.36, z = 1.14, NS		

SUMMER (LARGE SAMPLE)

Variable	Transformation	B	SE (B)	R	Mean percentage correct classifications (%)		
ALT (m)	$Log_{10}(x + 1)$	-8.90	3.35	-0.31	Absent	Present	Overall
VEG (wooded or non-wooded)	-	2.64	1.07	0.28	80.0	80.0	80.0
Constant	-	18.84	7.68		k = 0.58, z = 1.77, NS		

Table 5.3.9 continued

AUTUMN

Variable	Transformation	B	SE (B)	R	Mean percentage correct classifications (%)		
					Absent	Present	Overall
ALT (m)	$Log_{10}(x + 1)$	-5.75	2.57	-0.23			
VEG (wooded or non-wooded)	-	2.15	0.94	0.24	83.6	82.1	83.0
Constant	-	11.97	6.15		$k = 0.65$, $z = 2.02$, $p < 0.05$		

WINTER

Variable	Transformation	B	SE (B)	R	Mean percentage correct classifications (%)		
					Absent	Present	Overall
ALT (m)	$Log_{10}(x + 1)$	-8.46	3.05	-0.34			
Constant	-	18.99	7.06		90.3	57.1	81.0
					$k = 0.51$, $z = 1.30$, NS		

Table 5.3.10 Logistic regression models predicting the presence or absence of otter signs in 2.5km stretches of river from habitat variables in four surveys of the upper Tyne catchment between 1993 and 1995. B and SE (B) are the regression coefficients and standard errors for each variable, R is a measure of the partial correlation between the variable and the presence or absence of otter signs after all the other variables have been taken into account. The ability of the models to predict presence or absence of otter signs was tested by comparing the mean percentage of correct classifications in a 10 iteration cross-validation procedure with that expected if the models were predicting at random using Cohen's kappa.

SPRING (LARGE SAMPLE)

Variable	Transformation	B	SE (B)	R	Mean percentage correct classifications (%)		
					Absent	Present	Overall
ALT (≤200 or >200m)	-	-1.73	0.58	-0.27			
HOLT (pres/abs)	-	2.46	0.63	0.37	73.9	89.7	81.2
VEG1 (bare to <10cm)	-	-2.32	0.91	-0.22			
					k = 0.63, z = 2.60, p < 0.01		

Substituting LAG1 does not significantly improve the logistic model.

SUMMER (METALS SAMPLE)

Variable	Transformation	B	SE (B)	R	Mean percentage correct classifications (%)		
					Absent	Present	Overall
ALT (≤200 or >200m)	-	-3.07	1.08	-0.35			
Liver Cadmium (μg/g)	$Log_{10}(x + 1)$	2.15	0.81	0.32	64.6	83.3	73.3
LOACH1 (no stoneloach)	-	-2.92	1.41	-0.22			
					k = 0.47, z = 1.43, NS		

SUMMER (METALS SAMPLE) with LAG1

Variable	Transformation	B	SE (B)	R	Mean percentage correct classifications (%)		
					Absent	Present	Overall
ALT (≤200 or >200m)	-	-2.83	1.08	-0.31			
LAG1	-	3.22	1.17	0.34	65.6	85.0	73.3
					k = 0.47, z = 1.72, NS		

Table 5.3.10 continued

AUTUMN (LARGE SAMPLE)

Variable	Transformation	B	SE (B)	R	Mean percentage correct classifications (%)		
					Absent	Present	Overall
ALT (≤200 or >200m)	-	-3.08	0.74	-0.40	78.6	81.8	79.4
VEG4 (closed canopy)	-	2.47	0.91	0.23			
					k = 0.53, z = 1.93, NS		

AUTUMN (LARGE SAMPLE) with LAG1

Variable	Transformation	B	SE (B)	R	Mean percentage correct classifications (%)		
					Absent	Present	Overall
ALT (≤200 or >200m)	-	-2.64	0.63	-0.40	71.2	84.2	74.1
LAG1	-	2.92	0.75	0.37			
					k = 0.43, z = 1.60, NS		

WINTER (LARGE SAMPLE)

Variable	Transformation	B	SE (B)	R	Mean percentage correct classifications (%)		
					Absent	Present	Overall
ALT (≤200 or >200m)	-	-2.00	0.48	-0.40	76.7	75.0	75.3
					k = 0.45, z = 2.05, p < 0.05		

WINTER (LARGE SAMPLE) with LAG1

Variable	Transformation	B	SE (B)	R	Mean percentage correct classifications (%)		
					Absent	Present	Overall
ALT (≤200 or >200m)	-	-2.60	0.58	-0.51	73.8	84.1	77.6
LAG1	-	2.26	0.70	0.35			
					k = 0.44, z = 2.02, p < 0.05		

Table 5.3.11 Logistic regression models predicting the presence or absence of otter signs in 1km stretches of river from habitat variables in four surveys of the upper Tyne catchment between 1993 and 1995. B and SE (B) are the regression coefficients and standard errors for each variable, R is a measure of the partial correlation between the variable and the presence or absence of otter signs after all the other variables have been taken into account. The ability of the models to predict presence or absence of otter signs was tested by comparing the mean percentage of correct classifications in a 10 iteration cross-validation procedure with that expected if the models were predicting at random using Cohen's kappa.

SPRING (LARGE SAMPLE)

Variable	Transformation	B	SE (B)	R	Mean percentage correct classifications (%)		
WID4 (>20≤30m)	-	1.16	0.55	0.10	Absent	Present	Overall
VEG3 (>0.1≤1m)	-	-1.75	0.50	-0.20	57.3	71.6	61.8
PATH2 (>50≤150m)	-	-1.40	0.35	-0.23			
					k = 0.25, z = 1.67, NS		

Substituting LAG1 does not significantly improve the logistic model.

SUMMER (PREY SAMPLE)

Variable	Transformation	B	SE (B)	R	Mean percentage correct classifications (%)		
ALT1 (>50≤150m)	-	2.41	0.89	0.23	Absent	Present	Overall
ALT2 (>150≤225m)	-	1.86	0.69	0.23	90.8	76.5	86.2
MIN (presence/absence)	-	2.85	0.83	0.31	k = 0.68, z = 2.74, p < 0.01		
Constant	-	-3.95	0.88				

SUMMER (PREY SAMPLE) with LAG1

Variable	Transformation	B	SE (B)	R	Mean percentage correct classifications (%)		
MIN (pres/abs)	-	2.34	0.88	0.26	Absent	Present	Overall
LAG1	arcsine (x)	2.49	0.67	0.39	92.8	81.8	82.9
Constant	-	-3.34	0.84				
					k = 0.59, z = 2.32, p < 0.05		

Table 5.3.11 continued

AUTUMN (LARGE SAMPLE)

Variable	Transformation	B	SE (B)	R	Mean percentage correct classifications (%)		
					Absent	Present	Overall
ALT1 (>50≤150m)	-	2.07	0.52	0.27	95.8	40.7	83.3
DEP3 (>0.5≤1m)	-	1.65	0.47	0.23			
VEG3 (>0.1≤1m)	-	-1.78	0.78	-0.13	k = 0.37, z = 1.50. NS		
Constant	-	-1.96	0.29				

AUTUMN (LARGE SAMPLE) with LAG1

Variable	Transformation	B	SE (B)	R	Mean percentage correct classifications (%)		
					Absent	Present	Overall
LAG1	arcsine (x)	4.27	0.70	0.44	93.5	45.7	83.6
Constant	-	-2.91	0.37		k = 0.44. z = 1.91, NS		

WINTER (LARGE SAMPLE)

Variable	Transformation	B	SE (B)	R	Mean percentage correct classifications (%)		
					Absent	Present	Overall
WID4 (>20≤30m)	-	2.28	0.62	0.23	91.2	31.6	73.6
HOLT (pres/abs)	-	1.28	0.36	0.22			
Constant	-	-1.53	0.24		k = 0.26. z = 1.33. NS		

WINTER (LARGE SAMPLE) with LAG1

Variable	Transformation	B	SE (B)	R	Mean percentage correct classifications (%)		
					Absent	Present.	Overall
WID4 (>20≤30m)	-	1.80	0.72	0.15			
HOLT (pres/abs)	-	1.52	0.50	0.19			
LAG1	arcsine (x)	3.49	0.53	0.46	88.3	77.4	85.11
Constant	-	-1.53	0.24		k = 0.58, z = 1.17, NS		

Table 5.3.12 Logistic regression models predicting the presence or absence of otter signs in 600m stretches of river from habitat variables in four surveys of the upper Tyne catchment between 1993 and 1995. B and SE (B) are the regression coefficients and standard errors for each variable, R is a measure of the partial correlation between the variable and the presence or absence of otter signs after all the other variables have been taken into account. The ability of the models to predict presence or absence of otter signs was tested by comparing the mean percentage of correct classifications in a 10 iteration cross-validation procedure with that expected if the models were predicting at random using Cohen's kappa.

SPRING (LARGE SAMPLE)

Variable	Transformation	B	SE (B)	R	Mean percentage correct classifications (%)		
ALT1 (>50≤150m)	-	1.11	0.40	0.13	Absent	Present	Overall
WID1 (≤5m)	-	-2.16	0.75	-0.13	90.1	47.0	78.7
HOLT (pres/abs)	-	1.66	0.31	0.28	k = 0.40, z = 2.56, p < 0.05		
VEG2 (< 0.1m)	-	-0.90	0.44	-0.08			
Constant	-	-2.51	0.34				

SPRING (LARGE SAMPLE) with LAG1

Variable	Transformation	B	SE (B)	R	Mean percentage correct classifications (%)		
WID1 (≤5m)	-	-1.97	0.87	-0.10	Absent	Present	Overall
HOLT (pres/abs)	-	1.41	0.32	0.24	92.5	46.5	79.5
LAG1	arcsine (x)	2.49	0.47	0.30	k = 0.44, z = 2.86, p < 0.01		
Constant	-	-2.23	0.27				

SUMMER (PREY SAMPLE)

Variable	Transformation	B	SE (B)	R	Mean percentage correct classifications (%)		
MIN (pres/abs)	-	3.75	0.88	0.16	Absent	Present	Overall
LOACH2 (>0≤25 fish per $100m^2$)	-	2.15	0.73	0.27	86.3	72.1	82.0
VEG4 (woodland)	-	1.83	1.14	0.31	k = 0.58, z = 2.24, p < 0.05		
Constant	-	-5.08	1.25				

Table 5.3.12 continued

SUMMER (PREY SAMPLE) with LAG1

Variable	Transformation	B	SE (B)	R	Mean percentage correct classifications (%)		
MIN (pres/abs)	-	2.61	1.13	0.24	Absent	Present	Overall
LOACH2 (>0≤25 fish per 100m^2)	-	1.95	0.79	0.26	94.0	71.2	86.5
LAG1	arcsine (x)	2.07	0.66	0.36	k = 0.65, z = 2.47, p < 0.05		
Constant	-	-4.82	1.18				

AUTUMN (LARGE SAMPLE)

Variable	Transformation	B	SE (B)	R	Mean percentage correct classifications (%)		
ALT1 (>50≤150m)	-	1.43	0.40	0.21	Absent	Present	Overall
DEP3 (>0.5≤1m)	-	0.92	0.38	0.12	97.5	13.5	85.3
HOLT (pres/abs)	-	0.90	0.36	0.13	k = 0.25, z = 1.28, NS		
VEG6 (closed canopy woodland)	-	0.94	0.40	0.12			
Constant	-	-2.84	0.29				

AUTUMN (LARGE SAMPLE) with LAG1

Variable	Transformation	B	SE (B)	R	Mean percentage correct classifications (%)		
LAG1	arcsine (x)	5.82	0.78	0.46	Absent	Present	Overall
Constant	-	-3.19	0.32		95.8	27.7	85.8
					k = 0.29, z = 1.28, NS		

Table 5.3.12 continued

WINTER (LARGE SAMPLE)

Variable	Transformation	B	SE (B)	R	Mean percentage correct classifications (%)		
					Absent	Present	Overall
ALT1 (>50≤150m)	-	0.81	0.39	0.09	91.8	28.0	78.7
WID2 (>5≤10m)	-	-1.49	0.47	-0.16			
SUB3 (gravel/cobble)	-	0.83	0.32	0.12	k = 0.24, z = 1.29, NS		
HOLT (pres/abs)	-	1.22	0.32	0.20			
VEG6 (closed canopy woodland)	-	1.02	0.37	0.13			
Constant	-	-2.03	0.27				

WINTER (LARGE SAMPLE) with LAG1

Variable	Transformation	B	SE (B)	R	Mean percentage correct classifications (%)		
					Absent	Present	Overall
WID2 (>5≤10m)	-	-1.02	0.51	-0.08	88.4	44.6	80.4
SUB3 (gravel/cobble)	-	0.85	0.37	0.11			
HOLT (pres/abs)	-	0.96	0.37	0.13	k = 0.34, z = 1.90, NS		
LAG1	-	4.79	0.68	0.41			
Constant	-	-3.18	0.39				

Table 5.3.13 Logistic regression models predicting the presence or absence of otter signs in 200m stretches of river from habitat variables in four surveys of the upper Tyne catchment between 1993 and 1995. B and SE (B) are the regression coefficients and standard errors for each variable, R is a measure of the partial correlation between the variable and the presence or absence of otter signs after all the other variables have been taken into account. The ability of the models to predict presence or absence of otter signs was tested by comparing the mean percentage of correct classifications in a 10 iteration cross-validation procedure with that expected if the models were predicting at random using Cohen's kappa.

SUMMER (LARGE SAMPLE)

Variable	Transformation	B	SE (B)	R	Mean percentage correct classifications (%)		
ALT1 (>50≤150m)	-	0.92	0.27	0.14	Absent	Present	Overall
SUB4 (boulder & bedrock)	-	0.73	0.27	0.10	96.1	7.2	77.0
VEG5 (open canopy)	-	1.41	0.30	0.20	k = 0.31, z = 1.94, NS		
VEG6 (closed canopy)	-	1.79	0.31	0.25			
Constant	-	-2.75					

SUMMER (LARGE SAMPLE) with LAG1

Variable	Transformation	B	SE (B)	R	Mean percentage correct classifications (%)		
VEG5 (open canopy woodland)	-	1.00	0.32	0.13	Absent	Present	Overall
VEG6 (closed canopy woodland)	-	1.22	0.33	0.16	93.7	31.1	81.0
LAG1	arcsine (x)	5.12	0.62	0.38	k = 0.30, z = 2.01, p < 0.05		
Constant	-	-3.54	0.31				

Table 5.3.13 continued

AUTUMN (LARGE SAMPLE)

Variable	Transformation	B	SE (B)	R	Mean percentage correct classifications (%)		
					Absent	Present	Overall
SUB4 (boulder & bedrock)	-	0.80	0.29	0.12			
HOLT (pres/abs)	-	0.99	0.31	0.15	100	0	86.8
Constant	-	-2.29	0.18				

k = 0, z = 0, NS

AUTUMN (LARGE SAMPLE) with LAG1

Variable	Transformation	B	SE (B)	R	Mean percentage correct classifications (%)		
					Absent	Present	Overall
HOLT (pres/abs)	-	0.86	0.34	0.11			
LAG1	arcsine(x)	6.58	0.89	0.38	97.2	8.8	84.2
Constant	-	-3.38	0.28				

k = 0.09, z = 0.47, NS

WINTER (LARGE SAMPLE)

Variable	Transformation	B	SE (B)	R	Mean percentage correct classifications (%)		
					Absent	Present	Overall
ALT1 (>50≤150m)	-	1.03	0.24	0.18			
Constant	-	-1.50	0.13		100	0	97.1

k = 0, z = 0, NS

WINTER (LARGE SAMPLE) with LAG1

Variable	Transformation	B	SE (B)	R	Mean percentage correct classifications (%)		
					Absent	Present	Overall
LAG1	arcsine (x)	5.02	0.54	0.40			
Constant	-	-2.72	0.22		94.2	39.2	82.5

k = 0.39, z = 2.75, $p < 0.01$

5.3.2 Comparing North Tyne with South Tyne.

Correlations between environmental variables and catchment

Tables 5.3.14 to 5.3.16 show those variables that were correlated with the catchment dummy variables which have a component of their coefficients which was not explained by their correlation with any other predictor variables at the 1km, 600m and 200m sample unit sizes in the Summer and Autumn surveys only.

Table 5.3.14 Significant Pearson product-moment correlation coefficients between environmental variables and 1km stretches classified as North or South Tyne catchments in Summer and Autumn surveys of the upper Tyne catchment between 1993 and 1994 Only those predictor variables which have a component of their correlation coefficient which is not explained by any other variables are given. * denotes significant at $p < 0.05$; ** denotes significant at $p < 0.01$. Liver Lead and Muscle Copper concentrations were log-transformed before analysis.

Variable	n	Summer	Autumn
WID4 (>20≤30m)	182	-	-0.28**
ALT4 (>300m)	182	-0.25**	-0.25**
HOLT (pres/abs)	182	-0.20**	-0.20**
VEG1 (bare ground)	182	-	-0.25**
VEG3 (>0.1≤1m)	182	0.21**	0.28**
BROADS (pres/abs)	182	-0.32**	-0.32**
BUILD3 (>1000≤3000m^2)	182	-	-0.21**
MIN (pres/abs)	83	0.59**	No data
Liver Lead (μg/g)	45	-0.60**	-0.60**
Muscle Copper (μg/g)	45	-0.56**	-0.56**

Table 5.3.15 Significant Pearson product-moment correlation coefficients between environmental variables and 600m stretches classified as North or South Tyne catchments in Summer and Autumn surveys of the upper Tyne catchment between 1993 and 1994 Only those predictor variables which have a component of their correlation coefficient which is not explained by any other variables are given. * denotes significant at $p < 0.05$; ** denotes significant at $p < 0.01$. Liver Lead and Muscle Copper concentrations were log-transformed before analysis.

Variable	n	Summer	Autumn
DEP4 (>1m≤1.5m)	304	0.22**	-
WID5 (>30m)	304	-	0.22**
SUB3 (cobble)	304	-0.20**	-0.20**
ALT5 (>400m)	304	-0.39**	-0.39**
HOLT (pres/abs)	304	-	-0.15*
VEG3 (>0.1≤1m)	304	-	0.21**
BROADS (pres/abs)	304	-	-0.28**
PATHS (pres/abs)	304	-0.23**	-0.23**
MIN (pres/abs)	79	0.59**	No data
Liver Lead (μg/g)	45	-0.67**	-0.67**
Muscle Copper (μg/g)	45	-0.48**	-0.48**

Table 5.3.16 Significant Pearson product-moment correlation coefficients between environmental variables and 200m stretches classified as North or South Tyne catchments in Summer and Autumn surveys of the upper Tyne catchment between 1993 and 1994 Only those predictor variables which have a component of their correlation coefficient which is not explained by any other variables are given. * denotes significant at $p < 0.05$; ** denotes significant at $p < 0.01$. Liver Lead and Muscle Copper concentrations were log-transformed before analysis.

Variable	n	Summer	Autumn
DEP1 (≤0.25m)	498	-0.26**	-
WID5 (>30m)	498	-	0.22**
SUB5 (boulders & bedrock)	498	-	-0.15*
ALT2 (>150≤225m)	498	0.20**	0.20**
ALT5 (>400m)	498	-0.35**	-0.35**
VEG1 (bare ground)	498	-0.13*	-
VEG3 (>0.1≤1m)	498	-	0.23**
BUILDS (pres/abs)	498	-0.17**	-0.17**
MIN (pres/abs)	72	0.61**	No data
Liver Lead (μg/g)	44	-0.68**	-0.68**
Muscle Copper (μg/g)	44	-0.47**	-0.47**

Logistic regression models

Tables 5.3.17 to 5.3.19 show the resultant logistic regression models for the 1km, 600m and 200m sample unit sizes in Summer and Autumn using the variables outlined in Tables 5.3.14 to 5.3.16. For each model the results of the cross-validation procedure are given. The mean coefficients for each variable calculated from the 10 iterations of the cross-validation differed from the coefficients in the full model by less than 15% in all runs except those models run on the metals sample. When the metals sample was used some coefficients differed by 25% suggesting that, due to the small sample sizes, the sub-sampling procedure was unstable. This was also demonstrated by the high coefficients and standard errors shown in the logistic models using the metal samples. Therefore, the

results of the logistic regression models using the heavy metals should be treated with caution as they may be affected by overfitting.

The results of the logistic models show a general pattern for all sample unit sizes. When heavy metal variables were not included in the logistic models the presence or absence of otter signs was predicted significantly better than chance in the summer. The variable MIN (presence or absence of minnows) displaced the majority of other variables and became an important predictor in the models (R greater than 0.4 at all sample unit sizes). However, when heavy metal variables were included in the logistic models prediction improved and at the 600m and 200m sample unit sizes no other variables were retained in the models. Lead and copper were the most important of the two heavy metals in distinguishing between catchments with lead giving the highest R values of the two at the 600m and 200m scales.

Table 5.3.17 Logistic regression models classifying 1km stretches of river as North or South Tyne from environmental variables in Summer and Autumn surveys of the upper Tyne catchment between 1993 and 1995. B and SE (B) are the regression coefficients and standard errors for each variable, R is a measure of the partial correlation between the variable and the catchment group after all the other variables have been taken into account. The ability of the models to correctly predict catchment membership was tested by comparing the mean percentage of correct classifications in a 10 iteration cross-validation procedure with that expected if the models were predicting at random using Cohen's kappa.

SUMMER (PREY SAMPLE)

Variable	Transformation	B	SE (B)	R	Mean percentage correct classifications (%)		
					S.Tyne	N.Tyne	Overall
BROADS (pres/abs)	-	-1.82	0.64	-0.23	81.8	72.1	76.7
MIN (pres/abs)	-	2.93	0.63	0.42			
Constant	-	-0.43	0.42				
					k = 0.54, z = 2.48, p < 0.05		

SUMMER (METALS SAMPLE)

Variable	Transformation	B	SE (B)	R	Mean percentage correct classifications (%)		
					S.Tyne	N.Tyne	Overall
BROADS (pres/abs)	-	-3.93	1.96	-0.18	83.6	96.9	90.8
Liver Pb (μg/g)	$\log_{10}(x+1)$	-16.10	7.96	-0.18			
Muscle Cu (μg/g)	$\log_{10}(x+1)$	-38.69	17.90	-0.21			
Constant	-	21.68	9.80		k = 0.82, z = 2.84, p < 0.01		

AUTUMN (METALS SAMPLE)

Variable	Transformation	B	SE (B)	R	Mean percentage correct classifications (%)		
					S.Tyne	N.Tyne	Overall
Liver Pb (μg/g)	$\log_{10}(x+1)$	-10.24	3.94	-0.28	78.9	95.9	88.3
Muscle Cu (μg/g)	$\log_{10}(x+1)$	-27.42	10.90	-0.27			
Constant	-	13.59	4.94		k = 0.75, z = 2.50, p < 0.05		

Table 5.3.18 Logistic regression models classifying 600m stretches of river as North or South Tyne from environmental variables in Summer and Autumn surveys of the upper Tyne catchment between 1993 and 1995. B and SE (B) are the regression coefficients and standard errors for each variable, R is a measure of the partial correlation between the variable and the catchment group after all the other variables have been taken into account. The ability of the models to correctly predict catchment membership was tested by comparing the mean percentage of correct classifications in a 10 iteration cross-validation procedure with that expected if the models were predicting at random using Cohen's kappa.

SUMMER (PREY SAMPLE)

Variable	Transformation	B	SE (B)	R	Mean percentage correct classifications (%)		
PATHS (pres/abs)	-	-1.37	0.62	-0.17	S.Tyne	N.Tyne	Overall
MIN (pres/abs)	-	2.80	0.60	0.43	85.6	78.2	81.5
Constant	-	-0.63	0.43				

$k = 0.64$, $z = 2.86$, $p < 0.01$

SUMMER & AUTUMN (METAL SAMPLE)

Variable	Transformation	B	SE (B)	R	Mean percentage correct classifications (%)		
Liver Pb (μg/g)	$\log_{10}(x + 1)$	-7.50	2.43	-0.36	S.Tyne	N.Tyne	Overall
Muscle Cu (μg/g)	$\log_{10}(x + 1)$	-8.78	3.67	-0.25	80.0	90.0	85.5
Constant	-	9.00	2.65				

$k = 0.69$, $z = 2.25$, $p < 0.05$

Table 5.3.19 Logistic regression models classifying 200m stretches of river as North or South Tyne from environmental variables in Summer and Autumn surveys of the upper Tyne catchment between 1993 and 1995. B and SE (B) are the regression coefficients and standard errors for each variable, R is a measure of the partial correlation between the variable and the catchment group after all the other variables have been taken into account. The ability of the models to correctly predict catchment membership was tested by comparing the mean percentage of correct classifications in a 10 iteration cross-validation procedure with that expected if the models were predicting at random using Cohen's kappa.

SUMMER (PREY SAMPLE)

Variable	Transformation	B	SE (B)	R	Mean percentage correct classifications (%)		
BUILD (pres/abs)	-	-2.06	0.95	-0.17	S.Tyne	N.Tyne	Overall
MIN (pres/abs)	-	2.70	0.63	0.41	72.6	72.9	72.8
Constant	-	-0.74	0.43				
					$k = 0.49$, $z = 2.04$, $p < 0.05$		

SUMMER & AUTUMN (METAL SAMPLE)

Variable	Transformation	B	SE (B)	R	Mean percentage correct classifications (%)		
Liver Pb (μg/g)	$\log_{10}(x + 1)$	-8.61	2.75	-0.36	S.Tyne	N.Tyne	Overall
Muscle Cu (μg/g)	$\log_{10}(x + 1)$	-9.68	3.97	-0.26	80.0	90.9	85.5
Constant	-	10.03	2.93				
					$k = 0.69$, $z = 2.25$, $p < 0.05$		

Table 5.3.20 shows that the presence or absence of minnows was highly correlated with the concentration of lead in eel tissues at all three sample unit sizes. The results of the electro-fishing survey showed that there were higher proportions of stretches with minnows present in the North Tyne than in the South Tyne (Table 5.3.21). It is argued that the high levels of lead contamination in the South Tyne may, therefore, be limiting the distribution of minnows in the catchment (see section 5.4)

Table 5.3.20 Pearson product-moment correlation coefficients between the presence or absence of minnows and concentrations of lead in eel tissues from samples collected during an electro-fishing survey of the upper Tyne catchment in the summer of 1995. ** denotes significant at $p < 0.01$.

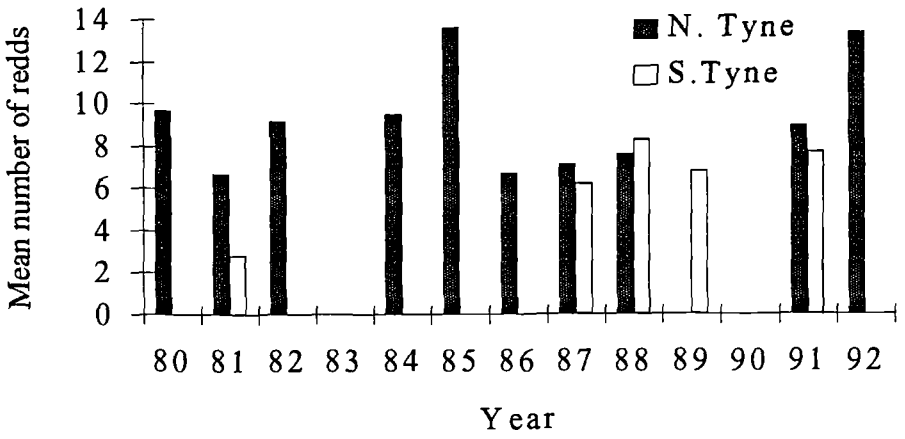
Sample unit size	Correlation coefficient
1km	-0.49**
600m	-0.60**
200m	-0.61**

Table 5.3.21 The proportion of stretches of river with minnow present during an electro-fishing survey of the upper Tyne catchment in the summer of 1995.

Sample unit size	Proportion of stretches with minnow present (%)	
	North Tyne	South Tyne
5km	83	27
2.5km	74	25
1km	79	19
600m	80	20
200m	80	19

Figure 5.3.1 shows that there were more sea trout redds in the South Tyne than in the North Tyne which may provide an explanation for the more widespread distribution of otter signs in the spring and winter seasons (see section 5.4)

Salmon



Sea Trout

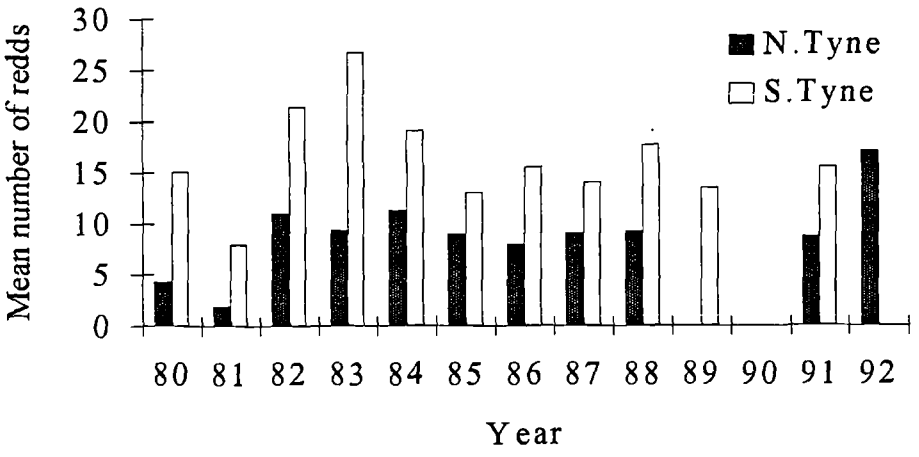


Figure 5.3.1 The mean number of salmon and trout spawning sites (redds) in North and South Tyne catchments between 1980 and 1992. Data from National Rivers Authority redd counts.

5.4 DISCUSSION

The majority of studies of otter habitat utilisation have used descriptive methods to compare stretches of riverbank with otter signs (or where otters spend more time) with other stretches where otter signs are less abundant or otter activity is lower (e.g. Macdonald & Mason, 1983; Durbin, 1993). However, these methods do not necessarily show a causal link between otter activity or the presence of otter signs and features of the habitat. Additionally, these studies often differ in their findings. For example, the majority of studies using spraint density surveys have concluded that there is a relationship with the availability of woodland on the riverbank (Mason & Macdonald, 1983; Bas *et al.*, 1984). Durbin (1993), on the other hand, found no such relationship but instead showed that the amount of time an otter spent in a particular area was related to physical characteristics such as river width and depth. The reasons for these differences may have been due not to the inefficiency of using spraint density surveys as Kruuk (1995) argued, but to the different studies including different variables in their analyses. For example, physical features of the watercourse were not generally considered in the majority of previous spraint density studies. Durbin (1993) argued that the relationship between otter activity and physical characteristics of the watercourse was due to selection for areas with high salmonid densities. It is possible that the relationship with woodland may also be secondary to the availability of prey, as many fish species prefer habitats with overhanging vegetation for cover (e.g. Raleigh *et al.*, 1986). In fact, the Tweed Foundation (which is working to conserve salmonid fisheries in the river Tweed) bases much of its management strategy on the provision of good bankside habitat (Tweed Foundation, 1995). Therefore, the inclusion of a quantitative estimate of prey populations in models of habitat utilisation may reveal much more about the distribution of otters in riparian environments than riverbank vegetation or physical parameters.

No previous studies have taken the spatial distribution of otter spraints into account when modeling habitat utilisation yet, as was shown in chapter 4 and the studies of Jenkins and Burrows (1980) and Trowbridge (1983), they are clearly not uniformly distributed, in neither coastal nor riparian habitats. By incorporating spatial effects into models of habitat utilisation more information is provided on the processes underlying

the distribution of otter signs. In addition the non-independence of sampling units due to spatial autocorrelation can be taken into account.

In the present study, predictive logistic regression models were used to provide more information on the causal processes determining the distribution of otter signs in the upper Tyne catchment. The rationale behind the choice of predictive models was that if the distribution of otter signs is caused by particular environmental parameters, then it should be possible to predict that distribution using those parameters. An autologistic approach was also taken which included covariates describing the spatial distribution of otter signs at a number of distances between sampling units. The inclusion of such variables provided more information on the relative contribution of reactive (caused by environmental conditions) or interactive (caused by otter behaviour) spatial effects to prediction of the distribution of otter signs. The majority of logistic models in this study failed to predict presence or absence of otter signs. Some models did, however, predict presence or absence significantly better than chance although the number of statistical analyses carried out may have led to Type I errors. Therefore significance values of $p < 0.05$ must be treated with caution. Nevertheless, in those models that did predict presence or absence of otter signs significantly better than chance (at any sample unit size) altitude was an important predictor variable. This was particularly the case in the spring and winter seasons when otter signs were unlikely to be found at altitudes of greater than 200m. Otters may avoid these higher altitudes during the colder months due to thermo-regulatory constraints. Kruuk (1995) argues that otters do not have efficient thermo-insulation (such as a layer of blubber in seals) consequently they cool rapidly in water. This means that otters energetic requirements are large requiring a high food intake. In addition as Kruuk (1995) argues, otters spend a lot of time in a wet medium. This is energetically costly because of increased heat loss. Therefore, otters will need places to shelter in order to recover from foraging bouts such as safe holts or suitable above-ground resting sites. In the present study, some of those models that included altitude as a predictor variable also included variables indicating a preference for stretches with holt sites and with some riverbank vegetation cover. This presents some tentative evidence to confirm Kruuk's (1995) view that the distribution of otters may be restricted to some extent by energetic requirements. Melquist & Hornocker (1983) showed that *L. canadensis* also avoided high altitudes and argued that this was due to a lack of suitable den sites for shelter. Logistic regression models also correctly predicted

the presence or absence of otter signs in the summer 1km and 600m sample unit sizes. The presence of minnows and stoneloach were important predictors in these models. The importance of minnows in determining the distribution of otters is discussed in more detail below.

On the whole, however, the majority of logistic models failed to adequately predict presence or absence of otter signs in the upper Tyne catchment. In addition, the inclusion of spatial autocovariates in the models did not significantly improve their predictive power except at the 200m sample unit size. It is likely, therefore, that the failure of the models at the majority of sample unit sizes was due to non-spatial factors. These can be divided into four categories; statistical error, sampling error, scale effects and temporal factors. At the 5km and 2.5km sample unit sizes only a small number of stretches were surveyed and of these only a small proportion of stretches produced otter signs. Therefore, the logistic models were built and validated using only a small dataset. This may have resulted in statistical error, thus reducing the predictive power of the logistic models. In addition, sampling error may mean that some of the variables measured were not described accurately by the samples taken. In particular, prey availability estimates for 5km and 2.5km stretches were determined from the results of the electro-fishing survey which sampled a maximum of only three sites per 5km stretch and two per 2.5km stretch. It is well-established that fish populations show a significant degree of variability between locations due to microhabitat factors, so considerably more sites within a 5km stretch would have to be sampled to give an accurate estimate of fish populations in such large stretches (Bohlin *et al.*, 1989). In addition, for many of the species encountered during electro-fishing, only presence or absence was used in the logistic modeling process. This is obviously a very coarse estimate of fish abundance over such large survey stretches. Heavy metal concentrations were measured in only 50 eels which may also not have been representative of pollutant contamination in such long survey stretches. The size of sampling units may also have been inappropriate. 5km and 2.5km sample unit sizes may have been too large to determine fine-scale use of habitats by otters; alternatively, they may have been too small to assess large-scale differences in habitat utilisation. The 200m sample unit size may simply have been too small, resulting in habitat assessments at a much finer scale than that at which the otter may view its habitat. However, it is argued that the most significant non-spatial factor leading to the failure of the models was the result of temporal effects. The home-ranges of otters are

large (Kruuk, 1995) and individual otters cannot possibly occupy the whole of this area all of the time. Therefore, some parts of their range which would normally provide suitable habitats may not have produced any spraints during a survey period simply because the resident otter is in another part of its home range. This problem will become increasingly apparent at smaller sample unit sizes and may be overcome by surveying at sample scales equivalent to the size of otter home ranges. However, it would be difficult to obtain reasonable sample sizes at this scale due to the logistic constraints of surveying over such large distances.

At the 1km, 600m and 200m sample unit sizes all of the above non-spatial errors may apply to the modeling of habitat utilisation by otters. However, the inclusion of spatial covariates did improve the predictions of some of the logistic models (particularly at the 200m sample unit size). As already discussed, this may have been due to other spatially distributed habitat variables which were not included in this study but interactive effects may also have played a part. Such effects may result from the function of sprainting behavior which is not necessarily related to habitat utilisation. Sprainting may have any of a number of functions, such as communication between individuals for purposes of signaling sexual and social status (Mason & Macdonald, 1983) or for territorial marking (Erlinge, 1967). It is also possible that the message carried by spraints may only be short-lived as suggested by Kruuk (1992) who argued that spraints served to indicate that foraging areas were in use by an otter, thus preventing over-exploitation of resources. However, without further investigation of the exact role of scent communication in otters, these effects cannot currently be determined.

Although, the majority of logistic models failed to demonstrate any relationship between habitat or prey availability variables and the presence of otter signs in sample unit sizes of 5km or less, some evidence was presented which tentatively showed differences between catchments. It was shown in chapter 4 that there were significant differences between the North and South Tyne in the percentage occurrence of stretches with otter signs in the summer and autumn at the 1km, 600m and 200m sample unit sizes. To explain these differences and also to assess differences in otter habitat utilisation at much larger scales the two catchments were used to create a dummy variable with a value of 1 for the South Tyne (representing low percentage occurrence of stretches with otter signs) and 2 for the North Tyne (representing a high percentage occurrence of stretches with otter signs).

Logistic regression modeling was then used to determine whether any of the environmental variables studied could be used to predict catchment membership. A clear picture emerged. Prediction of catchment categories was significantly better than by chance alone for all three sample unit sizes in both seasons. The ability of the models to correctly predict the catchment category increased when prey availability data were included with the presence of minnow being the best predictor. However, when data on heavy metal concentrations in eel tissue were included, lead and copper became the best predictors of catchment membership to the exclusion of all other variables. This result should be treated with some caution due to the low sample sizes involved in the cross-validation procedure.

These findings do not provide a direct causal link between environmental parameters and the presence of otter signs at a catchment scale. However, combined with other information (as discussed below), the results provide reasonable evidence that heavy metal pollution may be having an effect on otter distribution in the upper Tyne catchment. It is well established that heavy metal contamination can have direct toxic effects on many aquatic species including otters (Vernet, 1993; Mason, 1996). However, the exact impact of pollutants such as lead and copper on otter distribution is unknown. In the upper Tyne catchment the concentrations of lead and copper in eel tissues were used to predict whether sample stretches at the 1km, 600m and 200m sample unit sizes were in the South Tyne or the North Tyne. The mean concentrations of these metals were substantially higher in the South Tyne (Table VIII.VIIIa in Appendix VIII) which had significantly fewer stretches with otter signs in the summer and autumn. The implication of these results is that heavy metal pollution could be limiting the distribution of otters. If this was caused by direct toxic effects, it would be expected that the impact of this contamination on otter distribution would be the same regardless of the season. However, chapter 4 clearly shows that otter signs were widespread throughout both catchments in the spring and winter with no significant difference between the North and South Tynes in the proportions of stretches with otter signs. Therefore, if heavy metal pollution is having an impact on otter populations in these rivers its effect must be seasonal. The results of the logistic models of catchment membership without heavy metal data provide a clue to the mechanism of this seasonal factor. When the variables describing heavy metal contamination were excluded from the models the presence of minnows becomes the most significant predictor of catchment

membership. The presence of minnow was highly negatively correlated with the liver tissue concentrations of lead and at all three sample sizes (Table 5.3.20) suggesting that the presence of minnow was limited, directly or indirectly by lead contamination.

These results do not, however, provide evidence of a direct causal link between minnow availability and otter distribution unless it can be shown that minnow are important to the otter. Figure 4.3.2 in chapter 4 showed that minnows were an important component of the otters diet in all seasons. In fact, when percentage frequency was considered, minnow were as important as trout in the diet in most seasons. When relative frequency was considered minnow were the most important species in the otters diet in summer and autumn, reflecting closely their availability in the electro-fishing sample. The importance of minnow (in relative frequency terms) diminished considerably in the spring and winter, when trout were clearly the most important component of the diet. The results of the electro-fishing survey showed that the geographical distribution of minnow in the upper Tyne catchment was heavily skewed, with the majority of electro-fishing sites in the North Tyne containing minnow while in the South Tyne only a small proportion of sites contained minnow (Table 5.3.21). Therefore, since minnow were such an important component of the diet in the summer and autumn and were taken in proportion to availability, otters would need to use the North Tyne and lower reaches of the South Tyne in these seasons. This is exactly the distribution shown during the spraint surveys, with the majority of stretches producing otter signs clustered in these areas of the upper Tyne catchment (see chapter 3).

Why then are minnows so important to otters in the upper Tyne catchment in the summer and autumn periods and less so in the spring and winter? Erlinge (1968) and showed that "small cyprinids" were present in the otter's diet all year round but that they were caught in large numbers when they concentrated in the shallower shore areas. Melquist & Hornocker (1983) showed that small minnow-like species were also an important component of the diet of *L. canadensis* in Idaho. Minnows form huge spawning shoals in shallow water, often near the surface (pers. obs.), during the warmer months. In the winter they move to deeper water, taking shelter in small groups under bankside vegetation or under rocks. Therefore, minnows will form a highly abundant and available food source for otters in the summer and autumn but will be inactive and unavailable to otters in the colder months.

In the spring and winter, salmonids were the most important component of the otter's diet, perhaps as a result of the lack of availability of other species such as minnow, eel and stoneloach at this time as shown by other workers (e.g. Jenkins & Harper, 1980; Wise *et al.*, 1981). It is also likely that the proportion of large salmonids in the diet in these colder seasons was underestimated since the hard parts of large fish are often not ingested (Carss & Elston, 1996). However, Carss *et al.* (1990) showed that otters do prey on spawning adult salmonids. It is likely that in the colder months otters will take advantage of the availability of spawning salmonids, which may account for the increased proportion of stretches with otter signs found in the South Tyne in spring and winter. Figure 4.3.2 in chapter 4 showed that both salmon and trout were preyed on in the winter months. It is not known, however, what proportion of trout in the diet consists of migratory fish (sea trout). Analysis of annual spawning redd counts between 1980 and 1990 revealed that the South Tyne had considerably higher numbers of sea trout redds than the North Tyne (Figure 5.3.1) and that these were concentrated in the upper reaches of the catchment. Counts of salmon redds in the South Tyne were available only for some years but between 1987 and 1991 numbers appeared to be similar to those in the North Tyne. Therefore, if as shown in chapter 4, otters are taking prey in proportion to availability and trout form the highest component of the diet, the increased percentage of stretches with otter signs in the South Tyne in the winter and spring is likely to be the result of otters moving into this catchment to take advantage of the high number of spawning sea trout in this river in these seasons.

Seasonal changes in spraint density may be the result not only of the presence of cubs or the dispersal of young as suggested in previous studies (Jenkins & Burrows, 1980; Macdonald & Mason, 1987). Instead, they may also be the result of the movement of otters to new foraging areas within a catchment. These geographical changes will not be detected if only short stretches of riverbank in a small part of the catchment are surveyed. If however, sample stretches are surveyed throughout the catchment in different seasons, as in the present study, large-scale changes in otter distribution in response to prey availability can be detected. It must be emphasised that these findings are based on the comparison of only two catchments and further work involving a large number of river catchments is required to confirm these conclusions.

6 GENERAL DISCUSSION AND OVERVIEW

6.1 INTRODUCTION

In this chapter I will attempt to draw together the key conclusions from this study of the habitat requirements of the upper Tyne otter population. The implications of this work and the significance of the results to the wider field of otter ecology will be discussed. The discussion will also emphasise the need for more research into methods of studying and monitoring otter populations which take account not only of the distribution of individual otters in small areas but also their relationship with other individuals over broad geographical ranges.

6.2 OTTER DISTRIBUTION - THE INFLUENCE OF PREY

The availability of suitable prey was shown to be one of the most important determinants of the broad-scale geographic distribution of otters in the upper Tyne catchment (see chapter 5). The availability of such prey also accounted for seasonal differences in this distribution. Kruuk *et al.* (1993) also showed that the abundance of prey was an important determinant of otter distribution. They argued that it was the abundance of predominantly brown trout that influenced the distribution of otters in the Dee catchment, Aberdeenshire and that very small fish (<40mm) were unimportant in the diet. In the upper Tyne catchment it was demonstrated that the relationship between the distribution of otters and prey was complex and affected by seasonal factors. It was shown that otters do in fact take very small fish (<55mm) In particular minnows were taken in proportion to availability. It was also clearly demonstrated that the geographical distribution of otter signs in the upper Tyne catchment was almost identical to the distribution of minnows in the summer and autumn months when they were most abundant. In these seasons otter signs were virtually absent from the upper reaches of the South Tyne which reflected a lack of minnows in this part of the catchment. In the spring and winter however, otter signs were widespread throughout both catchments. It was shown that in these seasons, when minnows were unavailable, otters consumed predominantly salmonids. It was argued that his led to an increase in the range of otters to take advantage of the abundance of migratory salmonids, particularly sea trout, which were spawning in the upper reaches of the South Tyne.

Seasonal variations in prey abundance which effect the spatio-temporal distribution of otters in the Tyne catchment may have a profound impact on social structures. Kruuk (1995) argues that when a resource patch is rich enough to be shared by several otters conflicts between otters may occur. In addition, the linearity of the habitat also makes confrontation inevitable. Kruuk (1995) argues, therefore, that otters have two options in overcoming these problems - random dispersion, with tolerance between individuals or group territoriality. He argues that random dispersion without territoriality is uncommon in carnivores suggesting that phylogenetic constraints have prevented this spatial system from occurring. Kruuk (1995) concludes from studies in Shetland and Deeside that otters have developed a territorial arrangement in which several individuals share a range, each with its own favourite hunting haunts. However, there are exceptions to this pattern in different areas (e.g. Erlinge, 1968a) and in different species (Melquist & Hornocker, 1983). Kruuk & Moorhouse (1991) argued that the Resource Dispersion Hypothesis (RDH) may provide an explanation for these differences. Essentially, the existence of group territories is an adaptation to the availability of resources occurring in small temporal patches. Each individual requires a number of these patches within its range but because the patches are rich shares them with other individuals without competition. In the present study we have shown that there are large geographic and seasonal variations in the distribution of otters in the upper Tyne catchment which are dependent on the availability of prey in different areas. If otters occurred in group territories in the upper Tyne then they would have to be extremely large to cover both minnow and salmonid foraging areas. Alternatively, the geographical area of the group territory may change from one season to the next to exploit different patches. A more realistic explanation may be that otters in the Tyne have core areas such as the lower reaches of the South Tyne and North Tyne which they may occupy as group or individual territories. In the winter and spring, this pattern may break down as otters move into the upper reaches of the South Tyne to take advantage of the availability of salmonid prey on the spawning grounds. Tolerance to conspecifics may increase when prey is limited to particular geographic areas in these months. Increased foraging activity to cope with greater energetic requirements due to heat loss may also necessitate more tolerance between individuals in the colder seasons. This kind of breakdown in territoriality when foraging on salmonids was also demonstrated in *L. canadensis* populations in Idaho (Melquist & Hornocker, 1983). It is possible, therefore, that social

structure in otters is not as constrained by phylogenetic factors as Kruuk (1995) suggests. In fact, it may be more likely that otters have evolved a social structure that is adaptable to changing environmental conditions related to the patchy distribution of prey resources.

6.3 EFFECT OF ALTITUDE - THERMOREGULATORY CONSTRAINTS

Within their requirements for different prey in different seasons resulting in large spatio-temporal differences in distribution, this study also showed that, at smaller spatial scales otters avoided areas of high altitude. This was particularly the case in the summer and autumn with otter signs being more likely to be found in stretches of river at low altitudes (<200m) which had some riverbank vegetation cover with holt sites present. It was argued that this was due to the need for shelter while recovering from bouts of activity in the water. Some parts of the study area, particularly the upper reaches of the South Tyne were at high altitude (>600m) with watercourses running through open moorland and in some cases mountainous areas with snow cover often persisting into May. These areas were more inhospitable than valley habitats and afforded little protection from the elements. Given the thermo-regulatory difficulties of foraging in aquatic environments discussed by Kruuk (1995) it is unsurprising, therefore, that these areas are avoided in the colder months. These results demonstrate that a balance has to be maintained between the need to obtain the daily energetic requirements for survival against the energetic output required during foraging bouts. This energetic output will be determined partially by the need to stay warm in the water and the availability of suitable shelter when recovering from bouts of activity in cold water. By remaining in stretches of river at lower altitudes with suitable shelter in the winter months heat loss is reduced. However, during these months, the availability of prey is higher at salmonid spawning grounds which are mostly in the upper reaches of catchment. In this study it was shown that otter signs were more likely to be found at altitudes of less than 200m. This may be the altitude at which a balance is struck between the availability of migratory salmonids at spawning grounds in the upper reaches of the catchment and the energetic constraints of foraging in cold environments.

6.4 HEAVY METAL POLLUTION

This study is one of the first to show that heavy metal pollution may have an indirect impact on the distribution of otters. Tentative evidence was presented to suggest that lead pollution from abandoned mine-workings was limiting, either directly or indirectly, the distribution of minnows in the upper Tyne catchment. However, it should be emphasised that only a small sample size of eels was used to determine pollution levels and that the mechanism of the effects of this pollution on minnow populations are unknown. More research is needed before it can be definitively stated that heavy metal pollution is having a significant effect on minnow populations (and consequently otter distribution) in the Tyne catchment.

6.5 MONITORING OTTER POPULATIONS: TAKING ACCOUNT OF SPATIO-TEMPORAL VARIATIONS

This study has shown the importance of the catchment-wide approach in determining the habitat requirements of otters. The utilisation of habitats by otters in a small geographical area is clearly not independent of the availability of suitable habitats in other parts of the catchment. For example, if the movements of otters in a lowland stretch of river are studied in the summer a pattern of restricted foraging movements may be detected. However, in the late autumn, as prey such as minnow are no longer available, a pattern of transient movements may be detected with otters heading toward the headwaters of rivers to forage on salmonid spawning grounds. It is clear therefore, that studies of otter ecology must take account of spatio-temporal factors over a broad geographical. In addition, monitoring programmes should be designed to take account of seasonal variations in otter distribution. For example, if the upper reaches of the South Tyne had been surveyed in the summer using the national otter survey method it would have been concluded that otters did not occupy this section of river. However, if it had been surveyed in the winter it would have been concluded that this part of the catchment provided suitable habitats for otters. Neither of these conclusions reflect the true pattern of otter distribution in the upper Tyne catchment.

There are three main techniques currently in use for studying the ecology of wild otter populations. These are, (i) direct visual observations, (ii) radio-telemetry and, (iii)

surveys for otter spraints. Each method has its supporters and detractors and there has been considerable debate on the relative merits of one over the other (Jenkins & Burrows, 1980; Kruuk, *et al.*, 1986; Kruuk & Conroy, 1987; Mason & Macdonald, 1987).

Direct visual observation has been used with success to study the behaviour and ecology of otters inhabiting coastal areas of Shetland (see Kruuk, 1995 for review). In riparian habitats otters are predominantly nocturnal, occur at much lower population densities, have much larger home ranges and travel considerable distances within these (Erlinge, 1967a; Green, *et al.*, 1984; Durbin, 1993; Kruuk, *et al.*, 1993). In addition, riverbank structure and vegetation density often make access difficult to many sections of riverbank. Therefore, without considerable investment in human resources and night-vision equipment, it would be impractical to use visual observation as a method to determine habitat utilisation by otters in riparian habitats at a catchment scale.

The value of using radio-telemetry as a technique for studying otter behaviour and ecology has been well demonstrated (Melquist & Hornocker, 1983; Green *et al.*, 1984; Kruuk, 1995). Kruuk (1995) argued that radio-tracking is the only way to follow animals and to determine social interactions, foraging behaviour and habitat use. However, there are a number of disadvantages to the method. First, otters have to be trapped. Green *et al.* (1984) used Hancock livetraps to capture otters in Perthshire which resulted in two out of five otters escaping. These traps were however, successfully used by Melquist and Hornocker (1983) who tracked 39 otters over a five year period. There is no information on the period of time it took to trap otters in either of these papers but in Perthshire trapping success was estimated at one otter every three months (J. Green, pers. com.). If the density of otters in the Tyne is low, as believed by the Tyne Otter Forum, then trapping success may be even lower. Kruuk (1995) described a trap based on the design of the 'otter-house' used by Shetlanders to catch otters which were used with great success in Deeside, Aberdeenshire. However, the traps had to be left in place for many years without being set to allow otters to become habituated before trapping commenced. A second problem is that only small numbers of otters can be tracked over short periods of time. Green, *et al.* (1984) were only able to track three individuals (2 females and one male) for 22, 36 and 98 days respectively although they were able to increase their contact with the two females to 127 and 160

days using Zn^{65} to radio-label spraints. Kruuk *et al.* (1993) tracked eight otters (six males and two females) for periods of up to 13 months although only three otters were tracked for longer than 8 months. Durbin (1993) used the results from tracking only three otters to determine relationships between otter movements and habitat utilisation. Furthermore, it may be difficult in a heterogeneous habitat to determine the location of an animal using radio-telemetry with enough accuracy to identify the habitat type it occupies (Harris, Cresswell, Forde, Trewhella, Woollard & Wray, 1990). It is clear therefore, that radio-telemetry, can provide useful information on the behaviour and habitat use of a small number of individuals over short periods of time and in a limited geographical range. It is also clear, that collection of radio-tracking data is time-consuming and requires intensive resources which may not be available to organisations involved in otter conservation.

The most widely used technique in the study of otter ecology is the use of spraint density surveys (see reviews in Chanin, 1985 and Mason & Macdonald, 1986). These have been used in two ways. First, changes in the distribution of otters at regional and national scales have been determined using the presence of otter spraints in 600m stretches of watercourse at a number of sites within 10km grid squares (e.g. Strachan, Birks, Chanin, & Jefferies, 1990; Strachan & Jefferies, 1996). These surveys were conducted in 1977-79, 1984-86 and 1991-1993 and showed a gradual increase in the proportion of sites with otter signs over that period suggesting a recovery in otter populations since the major decline in the 1950s (Chanin & Jefferies, 1978). The use of spraint surveys provides probably the only method for assessing changes in otter distribution at this scale. However, seasonal factors are usually ignored in these regional or national surveys.

The extension of the spraint survey method to studies of habitat utilisation is more problematic, however, primarily because the exact function of sprainting and its relationship to otter activity is not fully understood (Kruuk, 1995). Despite this a substantial number of studies have used the abundance or presence of otter signs as an indicator of relative habitat utilisation (see Mason & Macdonald (1987) for review). The advantages of the method are that it is simple, does not require a large investment in human resources or equipment and large areas of river can be surveyed in a reasonable period of time enabling catchment-wide surveys. However, if the use of spraint surveys

is to be considered as a reliable method of determining habitat utilisation then it should be possible to find a combination of habitat parameters which predict a large proportion of the variation in the distribution of otter signs in a river catchment. If this is not the case then it would have to be concluded that other factors determine the distribution of otter signs and that spraint surveys cannot therefore be used in studies of habitat utilisation by otters. In this study it was demonstrated that the presence of otter signs in the upper Tyne catchment could be predicted from environmental variables and prey availability parameters in some seasons at sample unit sizes of less than 5km. However, the efficiency of these predictions was variable and only tentative conclusions could be drawn from the results. Comparisons of spraint densities between whole catchments may be a better method of determining the habitat requirements.

6.6 FUTURE RESEARCH

In this study it was demonstrated that spraint density surveys could be used to study differences between whole catchments. However, only two catchments were compared. Further research is needed which compares a much larger number of catchments. Many of the variables used in the present study were based on detailed field data and it would be impractical to collect these for a large number of catchments. However, there a many different projects working on otter populations in different areas which may already have such data available. In addition remotely sensed data such as satellite and aerial photographs may provide additional information. The availability of GIS and spatial analysis methods would assist in the handling of the large and complex datasets resulting from this kind of study.

A substantial amount of previous research has focused on the direct toxicity of pollutants on otter populations. Very little research has considered the indirect effects of pollutants on otter populations. In the present study heavy metal contamination may have had a limiting effect on otter distributions through its impact on minnow populations. However, sample sizes were small and there is a need for a much more detailed study of the mechanisms and impacts that pollutants have on the interactions between otters and their prey.

Kruuk (1995) also outlines some of the key future research that is required in order to answer some of the important questions in otter ecology and conservation. However, much of this research (and indeed, the two studies outlined above) will require reliable, easily applicable methods for determining otter distributions, population structure and changes in actual otter numbers. Despite much research these methods are still not available. Spraint distribution surveys may provide the most easily applicable method for studying otter distribution at a catchment-wide scale. However, the exact function of sprainting behaviour and how that relates to spraint distributions is still unknown. It is argued therefore, that one of the most important aspects of future research is to determine the function of otter sprainting, how it relates to the signalling of resources and to use this information to improve the efficiency of spraint density surveys. This aspect of research is fundamental if we are to progress our understanding of otter ecology. In fact, there is a great need for research into methods for studying a large number of mammalian species which cannot be easily observed directly or tracked using telemetric devices (e.g. other mustelids) This research is of academic interest but is also essential if we are to monitor the status of mammalian populations and develop appropriate strategies for their conservation or management.

REFERENCES

Abel, P. D. & Green, D. W. J. (1981) *Ecological and toxicological studies on the invertebrate fauna of two rivers in the northern Pennine orefield.* In Say, P. J. & Whitton B. A. (eds.) Heavy Metals in Northern England: Environmental and Biological aspects. University of Durham 1981 109-211.

Adrian, M. I. & Delibes, M. (1987) Food habits of the otter (*Lutra lutra*) in two habitats of the Donaña National Park, SW Spain. *Journal of Zoology, London.* **212** 399-406.

Anselin, L. (1992) *SpaceStat Tutorial: A workbook for using SpaceStat in the analysis of spatial data.* Regional Research Institute, West Virginia University, Morgantown, WV.

Anselin, L. (1995) *SpaceStat Version 1.80: User's guide.* Regional Research Institute, West Virginia University, Morgantown, WV.

Aplin, G. (1983) *Order-neighbour analysis. Concepts and techniques in modern geography 36.* Geo Books, Norwich.

Augustin, N. H., Mugglestone, M. A. & Buckland, S. T. (1996) An autologistic model for the spatial distribution of wildlife. *Journal of Applied Ecology* **33** 339-347.

Bainbridge, R. (1958) The speed of swimming of fish as related to size and to the frequency and amplitude of the tail beat. *Journal of Experimental Biology* **35** 109-133.

Bas, N., Jenkins, D. & Rothery, P. (1984) Ecology of otters in northern Scotland V. The distribution of otter (*Lutra lutra*) faeces in relation to bankside vegetation on the River Dee in summer 1981. *Journal of Applied Ecology.* **21** 507-513.

Beja, P. R. (1991) Diet of otters (*Lutra lutra*) in closely associated freshwater, brackish and marine habitats in south-west Portugal. *Journal of Zoology, London.* **225** 141-152.

Bohlin, T., Hamrin, S., Heggberget, T. G., Rasmussen, G. & Saltveit, S. V. (1989) Electrofishing-Theory and practice with special emphasis on salmonids. *Hydrobiologia* **173** 9-43.

Brewis, J. M. & Bowler, K. (1983) A study of the dynamics of a natural population of the freshwater crayfish, *Austropotamobius pallipes*. *Freshwater Biology* **13** 443-452.

Buckland, S. T. & Elston, D. A. (1993) Empirical models for the spatial distribution of wildlife. *Journal of Applied Ecology* **30** 478-495.

Burrough, P. A. (1988) *Principles of Geographical Information Systems for Land Resource Assessment.* Clarendon, Oxford.

Carpenter, S. R. & Chaney, J. E. (1983) Scale of spatial pattern: four methods compared. *Vegetatio* **53** 153-160

Carss, D. N. & Elston, D. A. (1996) Errors associated with otter *Lutra lutra* faecal analysis. II. Estimating prey size distribution from bones recovered in spraints. *Journal of Zoology, London.* **238** 319-332.

Carss, D. N. & Parkinson, S. G. (1996) Errors associated with otter *Lutra lutra* faecal analysis. I. Assessing general diet from spraints. *Journal of Zoology, London.* **238**, 301-317.

Carss, D. N., Kruuk, H. & Conroy, J. W. H. (1990) Predation on adult Atlantic salmon, *Salmo salar* L., by otters, *Lutra lutra* (L.), within the River Dee system, Aberdeen shire, Scotland. *Journal of Fish Biology.* **37** 935-944.

Chanin, P. R. F. (1985) *The Natural History of Otters.* Christopher Helm, Kent.

Chanin, P. R. F. & Jefferies, D. J. (1978) The decline of the otter *Lutra lutra* L. in Britain: an analysis of hunting records and discussion of causes. *Biological Journal of theLinnean Society.* **10** 305-328.

Chou, Y-H., Minnich, R. A., Salazar, L. A., Power, J. D. & Dezzani, R. J. (1990) Spatial autocorrelation of wildfire distribution in the Idyllwild Quadrangle, San Jacinto Mountain, California. *Photogrammetric Engineering & Remote Sensing* **56** 1507-1513.

Cliff, A. D. & Ord, J. K. (1973) *Spatial Autocorrelation.* Pion, London.

Cliff, A. D. & Ord, J. K. (1981) *Spatial processes: Models and applications.* Pion, London

Conroy, J. W. H. & French, D. D. (1987) The use of spraints to monitor populations of otters (*Lutra lutra* L). *Symposium of the Zoological Society of London* **58** 247-262.

Conroy, J. W. H., Watt, J., Webb, J. B. & Jones, A. (1993) *A guide to the identification of prey remains in otter spraints. Occasional Publication of the Mammal. Society.* No. 16. The Mammal Society, London.

Coshall, P. (1989) *The application of non-parametric statistical tests in geography.* Concepts and Techniques in Modern Geography (CATMOG) 50. Environmental publications, Norwich.

Delibes, M. & Adrian, M. J. (1987) Effects of crayfish introduction on otter *Lutra lutra* food in the Donaña National Park, SW Spain. *Biological Conservation* **42** 153-159.

Delibes, M., Macdonald, S. M. & Mason, C. F. (1991) Seasonal marking, habitat and organochlorine contamination in otters (*Lutra lutra*): a comparison between catchments in Andalucia and Wales. *Mammalia* **55** 567-578.

Dubuc, L. J., Krohn, W. B. & Owen, R. B., Jr. (1990) Predicting the occurrence of river otters by habitat on Mount Desert Island, Maine. *Journal of Wildlife Management* **54** 594-599.

Durbin, L. (1993) *Food and habitat utilisation of otters (Lutra lutra L.) in a riparian habitat-the River Don in north-east Scotland.* PhD thesis, University of Aberdeen.

Durbin, L. (1996) Some changes in the habitat use of a free-ranging female *otter Lutra lutra* during breeding. *Journal of Zoology, London* **240**, 761-764.

Erlinge, S. (1967a) Home range of the otter *Lutra lutra*, L. in southern Sweden. *Oikos* **18** 186-209.

Erlinge, S. (1967b) Food habits of the fish-otter, *Lutra lutra* L., in south Swedish habitats. *Viltrevy* **4** 371-443.

Erlinge, S. (1968a) Territoriality of the otter *Lutra lutra* L. *Oikos* **19** 81-98.

Erlinge, S. (1968b) Food studies on captive otters *Lutra lutra* L. *Oikos* **19** 259-270.

Feltham, M. J. & Marquiss, M. (1989) The use of first vertebrae in separating, and estimating the size of, trout (*Salmo trutta*) and salmon (*Salmo salar*) in bone remains. *Journal of Zoology, London* **219** 113-122.

Foster, J. & Turner, C. (1991) Insects and otter diet. *The Entomologist* **110** 166-169.

Fotheringham, A. S. & Knudsen, D. C. (1987) *Goodness-of-fit statistics. Concepts and techniques in modern geography 46.* Geo Books, Norwich.

Goodall, W. (1952) Quantitiative aspects of plant distribution. *Biological. Review.* **27** 194-245

Goodall, W. (1974) A new method for the analysis of spatial pattern by random pairing of quadrats. *Vegetatio* **29** 135-146

Goodchild, M. F. (1986) *Spatial autocorrelation. CATMOG 47.* Geo books, Norwich.

Gould, P. R. (1970) Is statistix inferens the geographical name for a wild goose? *Economic Geography* **58** 177-196

Green, J. & Green, R. (1980) *Otter survey of Scotland 1977-79.* Vincent Wildlife Trust, London.

Green, J., Green, R. & Jefferies, D. J. (1984) A radio-tracking survey of otters *Lutra lutra* on a Perthshire river system. *Lutra* **27** 85-145.

Greig-Smith, P. (1952) The use of random and contiguous quadrats in the study of the structure of plant communities. *Annals of Botany, London* **16** 293-316.

Greig-Smith, P. (1964) *Quantitative plant ecology. Second Edition.* Butterworths, London.

Haile, S. M. (1992) *Report on the ecology of the River North Tyne and Kielder Forest streams.* Phase II Report, University of Newcastle-upon-Tyne.

Haile, S. M. (1993) *Electrofishing surveys in the Kielder Forest district.* Department of Chemical and Process Engineering, University of Newcastle-upon-Tyne.

Haile, S. M., James, A. & Sear, D. (1989) *The effects of Kielder Reservoir on the ecology of the River North Tyne.* Report to Northumbrian Water on completion of Phase I. University of Newcastle-upon-Tyne.

Haines-Young, R., Green, D. R. & Cousins, S. eds. (1993) *Landscape ecology and geographic information systems.* Taylor & Francis, London.

Haining, R. (1990) *Spatial data analysis in the social and environmental sciences.* Cambridge University Press, Cambridge.

Harper, R. J. (1981) Sites of three otter (*Lutra lutra*) breeding holts in fresh-water habitats. *Journal of Zoology, London* **195** 554-556.

Harris, S., Cresswell, W.J., Forde, P.G., Trewhella, W. J., Woollard, T. & Wray, S. (1990) Home-range analysis using radio-tracking data-a review of problems and techniques particularly as applied to the study of mammals. *Mammal Review.* **20** 97-123.

Hosmer, D. W. & Lemeshow, S. (1989) *Applied logistic regression.* John Wiley & Sons, New York.

Jefferies, D. J. (1969) Causes of badger mortality in eastern counties of England. *Journal of Zoology* **157** 429-436.

Jefferies, D. J. (1987) *The effects of angling interests on otters, with particular reference to disturbance.* In: Maitland, P. S. & Turner, A. K. (eds) Angling and wildlife in fresh waters. ITE Symposium 19 Stirling. Institute of Terrestrial Ecology.

Jefferies, D. J. (1989) The changing otter population of Britain 1700-1989. *Biological Journal of the Linnean Society* **38** 61-69.

Jefferies, D. J., Wayre, P. Jessop, R. M. & Mitchell-Jones, A. J. (1986) Reinforcing the native otter *Lutra lutra* population in East Anglia: An analysis of the behaviour and range development of the first release group. *Mammal Review* **16** 65-79.

Jenkins, D. (1980) Ecology of otters in northern Scotland I. Otter (*Lutra lutra*) breeding and dispersion in mid-Deeside, Aberdeenshire in 1974-79. *Journal of Animal Ecology* **49** 713-735.

Jenkins, D. & Burrows, G. O. (1980) Ecology of otters in northern Scotland. III. The use of faeces as indicators of otter (*Lutra lutra*) density and distribution. *Journal of Animal Ecology* **49** 755-774.

Jenkins, D. & Conroy, J. W. H. (1981) Methodology for studying habits used by coastal otters. *Annual Report of the Institute of Terrestrial Ecology*. 19-22.

Jenkins, D. & Harper, R. J. (1980) Ecology of otters in northern Scotland II. Analyses of otter (*Lutra lutra*) and mink (*Mustela vison*) faeces from Deeside, N.E. Scotland in 1977-78. *Journal of Animal Ecology* **49** 737-754.

Jenkins, D., Walker, J. G. K. & McCowan, D. (1979) Analyses of otter (*Lutra lutra*) faeces from Deeside, N. E. Scotland. *Journal of Zoology, London* **187** 235-244.

Johnson, P. (1988) River regulation: a regional perspective-Northumbrian Water Authority. *Regulated Rivers and Management* **2** 233-255.

Kemenes, I. & Nechay, G. (1990) The food of otters *Lutra lutra* in different habitats in Hungary. *Acta theriologica* **35** 17-24.

Kershaw, K. A. (1957) The use of cover and frequency in the detection of pattern in plant communities. *Ecology* **38**: 291-299

Kozena, I., Urban, P., Stouracova, I. & Mazur, I. (1992) The diet of the otter (*Lutra lutra* Linn.) in the Polana Protected Landscape Region. *Folia zoologica* **41** 107-122.

Kruuk, H. (1992) Scent marking by otters (*Lutra lutra*) signalling the use of resources. *Behavioural Ecology* **3** 133-140.

Kruuk, H. (1995) *Wild otters: Predation and Populations.* Oxford University Press, Oxford.

Kruuk, H. & Conroy, J. W. H. (1987) Surveying otter *Lutra lutra* populations: a discussion of problems with spraints. *Biological Conservation* **41** 179-183.

Kruuk, H. & Conroy, J. W. H. (1991) Mortality of otters *Lutra lutra* in Shetland. *Journal of Applied Ecology.* **28** 83-94.

Kruuk, H. & Moorhouse, A. (1991) The spatial organisation of otters (*Lutra lutra*, L.) in Shetland. *Journal of Zoology, London* **221** 621-637

Kruuk, H., Conroy, J. W. H. & Carss, D. N. (1993) *Otters, eels and contaminants.* Report to Scottish Natural Heritage. Institute of Terrestrial Ecology.

Kruuk, H., Carss, D. N. Conroy, J. W. H. & Durbin, L. (1993) Otter (*Lutra lutra* L.) numbers and fish productivity in rivers in north-east Scotland. *Symposium of the Zoological Society of London.* **65** 171-191.

Kruuk, H., Conroy, J. W. H., Glimmerveen, U. & Ouwerkerk, E. J. (1986) The use of spraints to survey populations of otters *Lutra lutra. Biological Conservation* **35** 187-194.

Kruuk, H., Moorhouse, A., Conroy, J. W. H., Durbin, L. & Frears, S. (1989) An estimate of numbers and habitat preference of otters *Lutra lutra* in Shetland, UK. *Biological Conservation.* **49** 241-254.

Kyne, M. J., Smal, C. M. & Fairley, J. S. (1989) The food of otters *Lutra lutra* in the Irish midlands and a comparison with that of mink *Mustela vison* in the same region. *Proceedings of the Royal Irish Academy.* **89B** 33-46.

L'Abee-Lund, J. H., Langeland, A. & Seagrov, H. (1992) Piscivory by brown trout *Salmo trutta* L. and Atlantic charr *Salvelinus alpinus* (L.) in Norwegian lakes. *Journal of Fish Biology* **41** 91-101.

Legendre, P. (1993) Spatial autocorrelation: trouble or new paradigm? *Ecology* **74** 1659-1673.

Liebhold, A. M., Rossi, R. E. & Kemp, W. P. (1993) Geostatistics and Geographic Information Systems in applied insect ecology. *Annual Review of Entomology* **38** 303-327.

Macdonald, S.M. (1983) The status of the otter (*Lutra lutra*) in the British Isles. *Mammal Review* **13** 11-23.

Macdonald, S. M. & Mason, C. F. (1983) Some factors affecting the distribution of otters. *Mammal Review* **13** 1-10.

Macdonald, S. M. & Mason, C. F. (1987) Seasonal marking in an otter population. *Acta theriologica* **32** 449-462.

Macdonald, S. M. & Mason, C. F. (1988) Observations on an otter population in decline. *Acta theriologica* **33** 415-434.

Macdonald, S. M., Mason, C. F. & Coghill, I. S. (1978) The otter and its conservation in the River Teme catchment. *Journal of Applied Ecology* 15 373-84.

Maitland, P. S. (1972) *Key to British freshwater fishes.* No. 27. Freshwater Biological Association.

Mann, R. H. K. & Beaumont, W. R. C. (1980) The collection, identification and reconstruction of lengths of fish prey from their remains in pike stomachs. *Fisheries. Management* **11** 169-172.

Mason, C. F. (1989) Water pollution and otter distribution: a review. *Lutra* **32** 97-131

Mason, C. F. (1993) Regional trends in PCB and pesticide contamination in northern Britain as determined in otter (*Lutra lutra*) scats. *Chemosphere* **26** 941-944.

Mason, C. F. (1996) *Biology of freshwater pollution. Third Edition.* Longman, Harlow.

Mason, C. F. & Macdonald, S. M. (1986) *Otters, conservation and ecology.* Cambridge University Press, Cambridge.

Mason, C. F. & Macdonald, S. M. (1987) The use of spraints for surveying otter *Lutra lutra* populations: an evaluation. *Biological Conservation.* **41** 167-177.

Mason, C. F. & Macdonald, C. F. (1993) *PCB and organochlorine pesticide residues in otter spraints; their significance for regional otter conservation strategies.* Report to the World Wide Fund for Nature UK.

Mason, C. F., Last, N. I. & Macdonald, S. M. (1986) Mercury, Cadmium and Lead in British otters. *Bulletin of Environmental Contamination and Toxicology.* **37** 844-849.

McFadden, Y. M. T. & Fairley, J. S. (1984) Food of otters *Lutra lutra* (L.) in an Irish limestone river system with special reference to the crayfish *Austropotamobius pallipes. Journal of Life Sciences Research, Dublin Society.* **5** 65-76.

Melquist, W. E. & Hornocker, M. G. (1983) Ecology of river otters in Idaho. *Wildlife Monographs.* **83** 1-60.

Milton, J. S. (1993) *Statistical methods in the biological and health sciences. 2nd Edition.* McGraw-Hill Inc. New York.

Moran, P. (1948) The interpretation on statistical maps. *Journal of the Royal Statistical Society B* **10** 243-251

Newton, I. (1986) *The Sparrowhawk.* Poyser, London

Norusis, M. J. (1993a) *SPSS for Windows. Base system User's Guide Release 6.0.* SPSS Inc. Chicago, USA.

Norusis, M. J. (1993b) *SPSS for Windows. Professional Statistics Release 6.0.* SPSS Inc. Chicago, USA.

Norusis, M. J. (1993c) *SPSS for Windows. Advanced Statistics Release 6.0.* SPSS Inc. Chicago, USA.

NRA (1991a) *Juvenile salmonid monitoring programme 1991 River North Tyne.* National Rivers Authority, Northumbria Region.

NRA (1991b) *Juvenile salmonid monitoring programme 1991. River South Tyne.* National Rivers Authority, Northumbria Region.

NRA (1992a) *Juvenile salmonid monitoring programme 1992. River North Tyne.* National Rivers Authority, Northumbria Region.

NRA (1992b) *Juvenile salmonid monitoring programme 1992. River South Tyne and Devils Water.* National Rivers Authority, Northumbria Region.

NRA (1994a) *Juvenile salmonid monitoring programme 1994. River Tyne system. River North Tyne.* National Rivers Authority, Northumbria Region.

NRA (1994b) *Juvenile salmonid monitoring programme 1994. River Tyne system. River South Tyne.* National Rivers Authority, Northumbria Region.

NRA (1995) *River Tyne Catchment Management Plan.* National Rivers Authority, Northumbria & Yorkshire Region.

NWT (1992) Northumberland Otter Survey. *Roebuck* **Apr-Sep 6** 7-9.

O'Neill, R. V., DeAngelis, D. L., Waide, J. B. & Allen, T. F. H. (1986) *A Hierarchical Concept of Ecosystems.* Princeton University Press, Princeton.

Osborne, P. E. & Tigar, B. J. (1992) Interpreting bird atlas data using logistic models: an example from Lesotho, Southern Africa. *Journal of Applied Ecology* **29** 55-62.

Pielou, E. C. (1964) *An introduction to mathematical ecology.* Wiley-Interscience, New York.

Raleigh, R.F., Zuckerman, L. D. & Nelson, P. C. (1986) Habitat suitability index models and instream flow suitability curves: brown trout, revised. *U.S. Fish & Wildlife Service Biological Report* **82.**

Reynolds, J. C. & Aebischer, N. J. (1991) Comparison and quantification of carnivore diet by faecal analysis: a critique, with recommendations, based on a study of the Fox *Vulpes vulpes. Mammal Review.* **21** 97-122.

Rowe-Rowe, D. T. (1977) Food ecology of otters in Natal, South Africa. *Oikos* **28** 210-219.

Say, P. J. & Whitton, B. A. (1981) *Chemistry and plant ecology of zinc-rich streams in the northern Pennines.* In Say, P. J. & Whitton B. A. (eds.) Heavy Metals in Northern England: Environmental and Biological aspects. University of Durham 1981 55-63.

Shelley, J., Ferry, S. & Peacham, R. (1993a) *Juvenile salmonid monitoring programme 1993. River Tyne system. River North Tyne.* National Rivers Authority, Northumbria Region.

Shelley, J., Ferry, S. & Peacham, R. (1993b) *Juvenile salmonid monitoring programme 1993. River Tyne system. River South Tyne.* National Rivers Authority, Northumbria Region.

Smith, P. A. (1994) Autocorrelation in logistic regression modelling of species' distributions. *Global Ecology and Biogeography Letters* **4** 47-61.

Sokal, R. R. & Oden, N. L. (1978a) Spatial autocorrelation in biology 1. Methodology. *Biological Journal of the Linnean Society.* **10** 199-228.

Sokal, R. R. & Oden, N. L. (1978b) Spatial autocorrelation in biology 2. Some implications and four applications of evolutionary and ecological interest *Biological Journal of the Linnean Society.* **10** 229-249.

Southwood, T. R. E. (1977) *Ecological Methods.* Chapman & Hall, London.

Strachan, R. & Jefferies, D. J. (1996) *Otter survey of England 1991-1994.* Vincent Wildlife Trust, London.

Strachan, R., Birks, J. D. S., Chanin, P. R. F. & Jefferies, D. J. (1990) *Otter survey of England 1984-86.* Nature Conservancy Council, Peterborough.

Tabachnick, B. G. & Fidell, L. S. (1996) *Using multivariate statistics. 3rd Edition.* Harper Collins, New York.

Taylor, J. C. & Blackmore, D. K. (1961) A short note on the heavy mortality in foxes during the winter 1959-1960. *Veterinary Record* **73** 232-233.

Thom, T. J. (1989) *The ecology of otters (Lutra lutra) on the Wansbeck and Blyth river catchments in Northumberland.* Msc thesis, University of Durham.

Thom, T. J. (1995) *The Upper Tyne Otter Conservation Plan.* University of Durham, 1995.

Thom, T. J., Thomas, C. J., Dunstone, N. & Evans, P. R. (in press) The relationship between riverbank habitat and prey availability and the distribution of otter (*Lutra lutra*)

signs:- an analysis using a geographical information system. *Symposium of the Zoological Society, London* **71**

Tobler, W. R. (1970) A computer movie simulating urban growth in the Detroit region. *Economic Geography* **46** 234-240.

Trowbridge, B. J. (1983) Olfactory communication in the European otter *Lutra lutra*. PhD thesis. University of Aberdeen.

Tweed Foundation (1995) *Habitat Enhancement Project. 1994/1995 Progress Report.* Tweed Foundation.

Vernet, J.-P. (1992) *Impact of heavy metals on the environment. Trace metals in the environment 2.* Elsevier, Amsterdam.

Walter, S. D. (1993) Visual and statistical assessment of spatial clustering in mapped data. *Statistics in Medicine* **12** 1275-1291.

Webb, J. B. (1980) *Otter spraint analysis. Occasional Publication of the Mammal Society.* The Mammal Society, Reading.

Weber, J. M. (1990) Seasonal exploitation of amphibians by otters (*Lutra lutra*) in north-east Scotland. *Journal of Zoology., London.* **220** 641-651.

Wiedemann, C. F. & Fenster, C. A. (1978) The use of chance corrected percentage of agreement to interpret the results of discriminant analysis. *Educational Psychology Measurements.* **38** 29-35.

Wiens, J. A. (1989) Spatial scaling in ecology. *Functional Ecology* **3** 385-397

Wise, M. H. (1978) *The feeding ecology of otters and mink in Devon.* PhD thesis, University of Exeter.

Wise, M. H. (1980) The use of fish vertebrae in scats for estimating prey size of otters and mink. *Journal of Zoology, London.* **192** 25-31.

Wise, M. H., Linn, I. J. & Kennedy, R. (1981) A comparison of the feeding biology of mink *Mustela vison* and otter *Lutra lutra*. *Journal of Zoology, London.* **195** 181-213.

APPENDIX I THE TYNE OTTER FORUM

The Tyne Otter forum was established in 1990 to develop a strategy for the conservation of the European otter (*Lutra lutra*) in the River Tyne catchment in Northumberland, England. The Forum consisted of representatives from Northumbrian Water Ltd., the National Rivers Authority, Northumberland National Park, Northumberland Wildlife Trust, English Nature and Forest Enterprise-Kielder District.

The Forum considered that the distribution of otters in the River Tyne catchment was poorly understood and conservation measures could not be implemented until more information was made available on the factors affecting this distribution. Of particular interest were the reasons for the apparently lower numbers of otter signs found in the River South Tyne in comparison to the North Tyne during county-wide volunteer surveys conducted by Northumberland Wildlife Trust (NWT, 1992). It was decided, therefore, to provide consortium funding to establish a research programme based at the University of Durham to conduct a detailed study of the factors influencing the distribution of otters in the Tyne catchment. The ultimate aim of this research was to produce an otter conservation plan for the Tyne catchment and this was completed in 1995 (Thom, 1995).

APPENDIX II METHODS FOR DESCRIBING PATTERNS IN DISTRIBUTIONS.

The description of patterns in the distribution of a set of objects or species depends on a number of parameters which will influence the final outcome of an investigation. Southwood (1977) suggested that, when a population is sampled, three basic bits of information are available to describe that population; (i) the estimate ($\bar{x}$) of the true mean, μ, (ii) the estimate (s^2) of the true variance σ^2 and, (iii) the size of the sampling unit. Initial attempts to measure pattern in the distribution of species or objects were derived from various arrangements of this information. These were usually based on whether the observed distribution differed significantly from a Poisson (random) distribution, and, if so, whether the pattern of this distribution tended towards an aggregated (contagious or clumped) or a regular distribution (Greig-Smith, 1964; Pielou, 1969 and Southwood, 1977). These initial methods provided a description of pattern based on a single index usually derived from the variance to mean ratio which is unity for a Poisson distribution. When the variance is less than the mean a more regular distribution is implied although it is commoner to find a variance larger than the mean in ecological studies, that is, distributions which are clumped. The significance of the departure from random of a distribution can be determined by comparing the observed distribution with a Poisson distribution of the same mean and sample size using a standard goodness-of-fit test (Fotheringham & Knudsen, 1987). Alternatively the Index of Dispersion (I_D) can be used where,

$$I_D = \frac{s^2(n-1)}{\bar{x}} \qquad (n = \text{number of samples})$$

I_D is approximately distributed as χ^2 with n-1 degrees of freedom, so that if the distribution is random the value of I_D will not lie outside the limits (taken as 0.05 and 0.95) of the χ^2 distribution as given in standard tables.

An alternative approach is to utilise the negative binomial (Pascal) distribution which describes a clumped distribution. The distribution is described by two parameters, the mean and the exponent k, which is a measure of the amount of clumping and is often referred to as the dispersion parameter (Southwood, 1977). Generally, values of k are in

the region of 2; as they become larger the distribution approaches, and is eventually (at infinity) identical with, that of a Poisson distribution.

Goodall (1974) argued that random distributions were exceptional in ecological systems and that most sets of observations exhibited some form of aggregation. It was also suggested that the possible types of pattern were far too diverse to be described by a single index or a bare statement that it was aggregated. If in fact, the distribution was not random then the pattern required a much more detailed quantitative description. This description can be provided by two methods - quadrat analysis (Greig-Smith, 1952; Goodall, 1952) and order-neighbour analysis (Southwood, 1977; Aplin, 1983).

Quadrat analysis methods depend on quantitative records of plants or objects in quadrats constituting a two-dimensional grid or transect. The quadrats are combined in twos, fours, eights, etc., into blocks of successively larger size, and the values subjected to hierarchical analysis of variance (Greig-Smith, 1952; Kershaw, 1957). The variances between blocks are plotted against block size and the peaks and troughs of the resulting curves are interpreted as scales of pattern. The method has been widely used in plant ecology but a number of problems are generally recognised: (i) block sizes are restricted to integral sizes of two, (ii) results are affected by the starting position on the grid or transect (iii) variances at different spacings are not independent, and (iv) patches and gaps can be confounded (Goodall, 1974; Carpenter & Chaney, 1983). A considerable improvement in the method which overcame these problems and performed well in tests against other pattern analysis methods (Carpenter & Chaney, 1983) was the randomly paired quadrat method (Goodall, 1974). In this method the variances refer to mean spacings between quadrat centres on a linear transect rather than to block sizes. Instead of a hierarchical analysis of variance, independent variance estimates for each spacing between quadrats may be obtained by selecting random pairs of quadrats at a specified distance apart and using the difference between the members of the pair as a variance estimate with 1 degree of freedom. Once the variances at each spacing have been computed tests of significance can be applied, such as the F-test or, for the whole set of spacings, Bartlett's test (Milton, 1992).

A major drawback of quadrat based methods is that they only consider the frequency distributions of the number of points in a quadrat but do not consider how the quadrats

are distributed in relation to each other. Methods based on the distance between points, collectively known as order-neighbour analysis (Aplin, 1983) overcome this problem to a certain extent. A number of methods exist but the simplest involves the calculation of the R-statistic. In this method measurements are taken from a set of points to the first, second....., Kth nearest neighbouring points regardless of the direction of those measurements. The R-statistic describes the ratio of the mean of the observed point-to-point measures to the corresponding mean for random patterns. A random pattern is described by the value of $R(K) \approx 1$. Departure from random can be determined because we know that the distribution of R(K) values from random patterns approximates a normal distribution with a mean of 1 and a standard deviation which can be calculated for each K neighbour using formulae described by Aplin (1983). Critical values for a two-tailed test can then be calculated from tables of z-scores. Nearest neighbour measures give only limited information about the observed patterns. For example, if points are distributed as pairs, nearest neighbours may show a clumped distribution of individual points where in fact the pairs are distributed at random. By extending the analysis to the Kth nearest neighbour more information about observed patterns can be obtained. The interpretation of higher orders is limited to $K = 3$ since at $K > 3$ values of R(K) for the case of regularity or clustering fall within the ranges theoretically indicating randomness. Aplin (1983) also argued that the calculation of a single R(K) value constituted a considerable loss of information about the pattern. In addition, the calculation of R(K) depends on calculation of the density of points which is a function of area. In a riparian situation otter spraints are located on a narrow linear strip which therefore has no area making the calculation of R(K) impossible. To overcome these problems Aplin (1983) provides an alternative which does not require a measure of density and also provides a less ambiguous interpretation of higher order-neighbour analysis. Cumulative frequency analysis utilises the fact that we know that the values of R(K) follow a normal distribution with a known mean and standard deviation. We can use this information to calculate the expected cumulative frequencies at each of a number of z-scores or standard deviation unit values of a random distribution of nearest neighbours. This can then be compared with the cumulative frequency of the observed distribution of nearest neighbour distances using a goodness-of-fit test.

APPENDIX III DYNAMIC SEGMENTATION AND NETWORK ANALYSIS

The majority of data collected for this study described features of a 10m strip of riverbank (chapters 3 & 5). At a catchment-wide scale it is argued that these data describe a linear feature. To handle these kind of data in the GIS it was necessary to utilise software routines originally designed for management of linear networks. Arc/Info provides two groups of routines - Dynamic Segmentation and Network Analysis - specifically designed for storing, maintaining and analysing spatial data in linear networks.

Dynamic Segmentation uses a routes and measures dsystem for representing spatial data. In this system a linear feature is defined as a "route" which is constructed from whole or partial arcs in a coverage. Routes have a measurement system (measures) associated with them and attributes (called "events" in Arc/Info) can be positioned on routes using these measures. Two types of events can be identified; (i) point events, e.g. individual spraint locations, (ii) linear events, e.g. a length of riverbank of a particular vegetation type. Events are stored in database tables together with descriptive information on each event and are linked to the relevant route by a unique route identifier. Route systems can also be linked to information stored in co-ordinate based coverages by converting routes into arc or point coverages using Arc/Info routines.

In addition to the storage of linear spatial information, Dynamic Segmentation provides data in a format which can be used in Network Analysis. This is a powerful tool in Arc/Info which facilitates the analysis and modelling of spatial interactions between features in a linear system. In this thesis Network Analysis was used to create a matrices of distances between spraint locations for use in spatial autocorrelation analysis (see chapter 3).

APPENDIX IV SPATIAL AUTOCORRELATION ANALYSIS

IV. I INTRODUCTION

Spatial autocorrelation is concerned with the comparison of two types of information: similarity among attributes and similarity of location.

The following notation will be used in this Appendix;

n = number of sample units

i, j = any two of the sample units

z_i = the value of the attribute for sample unit i

c_{ij} = The similarity of i's and j's attributes

w_{ij} = the similarity of i's and j's locations

In general spatial autocorrelation compares the set of attribute similarities c_{ij} with the set of locational similarities w_{ij}.

IV. II MORAN'S I

Moran's I (Moran, 1948) is defined as

$$I = n/S_0 \, \Sigma_i \Sigma_j w_{ij}.(z_i - \mu).(z_j - \mu) / \Sigma_i (z_i - \mu)^2$$

where S_0 is a scaling constant = $\Sigma_i \Sigma_j w_{ij}$.

For a row-standardised matrix S_0 = n (since each row sums to 1). Moran's I is similar to a correlation coefficient and is not centered around zero but has a theoretical mean of

-1/n-1. Thus, the expected value is negative but tends to zero as the sample size increases. A Moran's I coefficient larger than its expected value indicates positive spatial autocorrelation, and a Moran's I less than its expected value indicates negative spatial autocorrelation. However, it is more usual to base inference on a standardised z-value. This is computed by subtracting the theoretical mean and dividing the result by the theoretical standard deviation. The values of the theoretical mean and standard deviation of Moran's I will vary depending on assumptions about the nature of the attribute and the nature of the spatial autocorrelation. Therefore, the value of z_i will also vary as will the interpretation of its significance. For normally distributed variables the z-value follows standard normal distribution and the significance of the statistic can be determined from comparison with values in a standard-normal table.

For non-normally distributed variables or variables where the form of the distribution is unknown a randomisation assumption can be used where it is assumed that each value could equally likely have occurred at all locations. Based on this assumption, different theoretical standard deviations will be obtained which yield different z-scores which again follow the standard normal distribution. Alternatively, rather than using a theoretical mean and standard deviation, a reference distribution for I can be generated empirically from which the mean and standard deviation are computed. This is carried out by randomly reshuffling the observed values over all locations and by re-computing the I statistic for each new sample. This is known as the permutation approach.

IV.III JOIN COUNTS

Join count statistics provide the simplest measure of spatial autocorrelation and are appropriate for binary variables which are usually expressed in terms of Black and White. Join counts are counts of the number of times a join, ie a contiguity corresponds to similar or dissimilar value in the neighbouring units. Three types of joins can be recognised; Black-Black (BB) joins, White-White (WW) joins (both eqivalent to positive autocorrelation) and Black-White (BW) joins (eqivalent to negative autocorrelation).

The join count statistics are;

$$BB = (1/2)\sum_i \sum_j w_{ij} x_i x_j$$

$$BW = (1/2)\sum_i \sum_j w_{ij} \left(x_i - x_j\right)^2$$

$$WW = (1/2)\sum_i \sum_j w_{ij} \left(1 - x_i\right)\left(1 - x_j\right)$$

where x = 1 for Black and x = 0 for White and w_{ij} is the i-jth element in the spatial weights matrix. Statistical inference is based on the permutation approach (see above). Full details of the join count method can be found in Goodchild (1986).

APPENDIX V RESULTS OF THE ANALYSIS OF SPATIAL PATTERNS IN THE DISTRIBUTION OF OTTER SIGNS IN THE UPPER TYNE CATCHMENT

Table V.I Moran's I indices of spatial autocorrelation (using a number of distance filters) of otter spraints (SIGN) and spraint sites (SITE) in 5km stretches of riverbank in four seasonal surveys of the upper Tyne catchment between March 1993 and November 1994. Pseudo-significance values (p) were estimated using a permutation approach (99 permutations) Significant values are highlighted in bold.

Season	Variable	Distance 1 (≥5<10km)		Distance 2 (≥10<20km)		Distance 3 (≥20<30km)		Distance 4 (≥30<40km)		Distance 5 (≥40<50km)		Distance 6 (≥50<75km)		Distance 7 (≥75≤100km)	
		I	p	I	p	I	p	I	p	I	p	I	p	I	p
Spr	SIGN	0.09	0.15	-0.04	0.50	-0.08	0.21	-0.04	0.51	0.01	0.33	-0.07	0.11	-0.07	0.22
	SITE	0.15	0.06	-0.03	0.48	-0.06	0.38	-0.06	0.32	0.01	0.36	-0.08	0.08	-0.08	0.16
Sum	SIGN	0.24	0.12	0.06	0.19	0.03	0.25	-0.16	0.04	0.03	0.24	-0.14	0.02	-0.09	0.15
	SITE	0.12	0.16	0.05	0.19	0.05	0.12	-0.16	0.04	-0.01	0.42	-0.12	0.04	-0.08	0.16
Aut	SIGN	-0.29	0.03	**0.16**	**0.01**	0.06	0.11	**-0.23**	**0.01**	-0.14	0.10	-0.10	0.04	-0.06	0.27
	SITE	-0.30	0.03	**0.16**	**0.01**	0.04	0.18	**-0.23**	**0.01**	-0.12	0.16	-0.08	0.12	-0.07	0.29
Win	SIGN	0.12	0.20	0.07	0.18	0.06	0.22	-0.18	0.04	-0.00	0.36	-0.13	0.08	-0.06	0.29
	SITE	0.08	0.21	0.08	0.16	0.03	0.29	-0.16	0.08	0.03	0.26	-0.12	0.10	-0.05	0.31

Table V.II Join count estimates of spatial autocorrelation (using a number of distance filters) of the presence or absence of otter signs in forty 5km stretches of riverbank in four seasonal surveys of the upper Tyne catchment between March 1993 and November 1994. BB joins are between two contiguous 5km stretches with otter signs present and BW joins are between two contiguous 5km stretches, where one 5km stretch has otter signs present and its neighbour has no otter signs. These analyses were carried out for each season. Pseudo-significance values (p) were estimated using a permutation approach (99 permutations) Significant values are highlighted in bold.

		Distance 1 (≥5<10km)		Distance 2 (≥10<20km)		Distance 3 (≥20<30km)		Distance 4 (≥30<40km)		Distance 5 (≥40<50km)		Distance 6 (≥50<75km)		Distance 7 (≥75≤100km)	
Season	Join	No.	p	No.	p	No.	p	No.	p	No.	p	No.	p	No.	p
Spr	BB	9	0.06	30	0.11	32	0.21	26	0.57	27	0.6	59	0.28	29	0.98
	BW	9	0.81	38	0.73	49	0.43	50	0.22	49	0.30	86	0.92	73	0.18
Sum	BB	**7**	**0.01**	15	0.13	18	0.05	16	0.11	13	0.5	23	0.75	10	0.98
	BW	9	0.65	41	0.33	47	0.35	50	0.09	46	0.46	97	0.09	60	0.82
Aut	BB	4	0.36	**22**	**0.01**	21	0.11	15	0.58	18	0.29	33	0.55	15	0.99
	BW	14	0.0[illegible]	38	0.76	50	0.32	53	0.08	42	0.84	92	0.53	69	0.45
Win	BB	2	0.49	11	0.05	11	0.15	9	0.3	10	0.29	14	0.75	8	0.90
	BW	11	0.19	39	0.21	43	0.35	47	0.07	40	0.52	89	0.06	44	1.00

Table V.III Join count estimates of spatial autocorrelation (using a number of distance filters) of the presence or absence of otter signs in seventy 2.5km stretches of riverbank in four seasonal surveys of the upper Tyne catchment between March 1993 and November 1994. BB joins are between two contiguous 2.5km stretches with otter signs present and BW joins are between two contiguous 2.5km stretches, where one 2.5km stretch has otter signs present and its neighbour has no otter signs.. Pseudo-significance values (p) were estimated using a permutation approach (99 permutations) Significant values are highlighted in bold.

		Distance 1 (≥2.3≤2.7km)		Distance 2 (≥5<10km)		Distance 3 (≥10<20km)		Distance 4 (≥20<30km)		Distance 5 (≥30<40km)		Distance 6 (≥40<50km)		Distance 7 (≥50<75km)		Distance 8 (≥75≤100km)	
Season	Join	No.	p	No.	p	No.	p	No.	p	No.	p	No.	p	No.	p	No.	p
Spr	BB	11	0.05	23	0.03	**74**	**0.01**	**75**	**0.01**	64	0.34	62	0.64	125	0.46	65	0.99
	BW	10	1.00	32	0.83	119	0.78	144	0.24	147	0.10	153	0.19	286	0.46	214	0.32
Sum	BB	**11**	**0.01**	15	0.10	45	0.03	48	0.04	40	0.35	35	0.72	77	0.47	38	0.95
	BW	5	1.00	40	0.07	129	0.02	137	0.14	134	0.22	147	0.15	257	0.84	191	0.72
Aut	BB	**7**	**0.01**	10	0.08	**32**	**0.01**	30	0.02	25	0.15	20	0.58	35	0.78	10	1.00
	BW	4	1.00	27	0.76	102	0.34	126	0.03	125	0.04	137	0.03	258	0.02	128	1.00
Win	BB	8	0.04	11	0.17	**42**	**0.01**	39	0.06	33	0.26	34	0.38	56	0.73	23	0.99
	BW	4	1.00	35	0.29	106	0.79	**145**	**0.01**	132	0.12	133	0.46	267	0.95	163	0.98

Table V.IV Join count estimates of spatial autocorrelation (using a number of distance filters) of the presence or absence of otter signs in 182 1km stretches of riverbank in four seasonal surveys of the upper Tyne catchment between March 1993 and November 1994. BB joins are between two contiguous 1km stretches with otter signs present and BW joins are between two contiguous 1km stretches, where one 1km stretch has otter signs present and its neighbour has no otter signs. Pseudo-significance values (p) were estimated using a permutation approach (99 permutations) Significant values are highlighted in bold.

		Distance 1 (≥0.8≤1.2km)		Distance 2 (≥2.8<3.2km)		Distance 3 (≥5<10km)		Distance 4 (≥10<20km)		Distance 5 (≥20<30km)		Distance 6 (≥30<40km)		Distance 7 (≥40<50km)		Distance 8 (≥50<75km)	
Season	Join	No.	p	No.	p	No.	p	No.	p	No.	p	No.	p	No.	p	No.	p
Spr	BB	**28**	**0.01**	14	0.02	**97**	**0.01**	191	0.03	195	0.29	181	0.30	192	0.45	362	0.56
	BW	37	1.00	27	0.99	262	0.28	776	0.02	**923**	**0.01**	850	0.03	802	0.86	1685	0.05
Sum	BB	**37**	**0.01**	**21**	**0.01**	**88**	**0.01**	**168**	**0.01**	167	0.06	174	0.02	142	0.36	228	0.97
	BW	11	1.00	12	1.00	246	0.14	**709**	**0.01**	**841**	**0.01**	**876**	**0.01**	807	0.15	**1713**	**0.01**
Aut	BB	**23**	**0.01**	**13**	**0.01**	**59**	**0.01**	**110**	**0.01**	106	0.04	93	0.03	90	0.33	125	0.98
	BW	18	1.00	15	1.00	207	0.20	589	0.08	713	0.02	**784**	**0.01**	705	0.06	**1465**	**0.01**
Win	BB	**36**	**0.01**	**23**	**0.01**	**95**	**0.01**	172	0.12	199	0.13	160	0.57	205	0.08	326	0.93
	BW	22	1.00	13	1.00	269	0.16	**829**	**0.01**	**894**	**0.01**	**906**	**0.01**	752	1.00	1688	0.04

Table V.V Join count estimates of spatial autocorrelation (using a number of distance filters) of the presence or absence of otter signs in 304 600m stretches of riverbank in four seasonal surveys of the upper Tyne catchment between March 1993 and November 1994. BB joins are between two contiguous 600m stretches with otter signs present and BW joins are between two contiguous 600m stretches, where one 600m stretch has otter signs present and its neighbour has no otter signs. Pseudo-significance values (p) were estimated using a permutation approach (99 permutations) Significant values are highlighted in bold.

		Distance 1 (≥1.1≤1.3km)		Distance 2 (≥2.3≤2.5km)		Distance 3 (≥3.5≤3.7km)		Distance 4 (≥5<10km)		Distance 5 (≥10<20km)		Distance 6 (≥20<30km)		Distance 7 (≥30<40km)		Distance 8 (≥40<50km)	
Season	Join	No.	p	No.	p	No.	p	No.	p	No.	p	No.	p	No.	p	No.	p
Spr	BB	**31**	**0.01**	**17**	**0.01**	11	0.04	**216**	**0.01**	**382**	**0.01**	412	0.08	391	0.03	368	0.50
	BW	54	1.00	46	1.00	23	1.00	685	0.03	**2102**	**0.01**	2249	**0.01**	**2187**	**0.01**	2110	0.40
Sum	BB	**33**	**0.01**	**22**	**0.01**	**11**	**0.01**	**176**	**0.01**	**282**	**0.01**	**267**	**0.01**	**240**	**0.01**	237	0.10
	BW	27	1.00	21	1.00	14	1.00	**607**	**0.01**	1657	0.02	1890	**0.01**	**2080**	**0.01**	**1913**	**0.01**
Aut	BB	**15**	**0.01**	**12**	**0.01**	8	0.02	**102**	**0.01**	**164**	**0.01**	**159**	**0.01**	123	0.15	126	0.24
	BW	46	1.00	27	1.00	14	1.00	**537**	**0.01**	**1327**	**0.01**	1560	**0.01**	**1612**	**0.01**	1518	0.02
Win	BB	**30**	**0.01**	**17**	**0.01**	7	0.18	**147**	**0.01**	**301**	**0.01**	290	0.22	241	0.59	289	0.21
	BW	43	1.00	39	1.00	22	0.98	**697**	**0.01**	**1928**	**0.01**	2029	**0.01**	**2049**	**0.01**	1833	0.66

Table V.VI Join count estimates of spatial autocorrelation (using a number of distance filters) of the presence or absence of otter signs in 498 200m stretches of riverbank in four seasonal surveys of the upper Tyne catchment between March 1993 and November 1994. BB joins are between two contiguous 200m stretches with otter signs present and BW joins are between two contiguous 200m stretches, where one 200m stretch has otter signs present and its neighbour has no otter signs. Pseudo-significance values (p) were estimated using a permutation approach (99 permutations) Significant values are highlighted in bold.

		Distance 1 (≥150≤250m)		Distance 2 (≥1.95≤2.05km)		Distance 3 (≥3.95≤4.05km)		Distance 4 (≥5<10km)		Distance 5 (≥10<20km)		Distance 6 (≥20<30km)		Distance 7 (≥30<40km)		Distance 8 (≥40<50km)	
Season	Join	No.	p	No.	p	No.	p	No.	p	No.	p	No.	p	No.	p	No.	p
Spr	BB	**66**	**0.01**	**30**	**0.01**	12	0.18	**700**	**0.01**	1204	0.06	1159	0.76	1161	0.26	1225	0.07
	BW	74	1.00	72	0.99	53	0.33	2360	0.02	5879	0.04	**6869**	**0.01**	5907	0.29	6002	0.07
Sum	BB	**40**	**0.01**	**21**	**0.01**	7	0.14	**447**	**0.01**	**705**	**0.01**	649	0.26	574	0.52	**713**	**0.01**
	BW	79	0.98	60	0.81	47	0.13	**2008**	**0.01**	4710	0.02	**5353**	**0.01**	**5188**	**0.01**	5000	0.02
Aut	BB	**51**	**0.01**	17	0.02	11	0.09	**413**	**0.01**	**917**	**0.01**	885	0.03	651	0.93	791	0.06
	BW	68	1.00	72	0.57	45	0.35	**2224**	**0.01**	**5463**	**0.01**	**5636**	**0.01**	**5599**	**0.01**	5184	0.08
Win	BB	**26**	**0.01**	9	0.02	**7**	**0.01**	**188**	**0.01**	**334**	**0.01**	**363**	**0.01**	233	0.71	278	0.15
	BW	56	1.00	50	0.28	32	0.22	**1550**	**0.01**	3342	0.21	3800	0.04	**3729**	**0.01**	**3687**	**0.01**

APPENDIX VI RESULTS OF DIETARY STUDIES FROM OTTER SPRAINT ANALYSIS

Table VI.I Percentage frequencies and relative frequencies of prey items (95% confidence intervals in brackets) found in otter spraints collected from the upper Tyne catchment in four seasonal surveys between 1993 and 1994 (all figures are percentages).

	Spring 1993		Summer 1993		Autumn 1994		Winter 1994		Overall	
Prey type	% freq.	Rel. freq.(%)	% freq.	Rel. freq.(%)	% freq.	Rel. freq.(%)	% freq.	Rel. freq.(%)	% freq.	Rel. freq.(%)
Salmon	35 (24-46)	26 (25-27)	24 (12-36)	13 (12-14)	28 (11-45)	9 (7-11)	35 (21-49)	24 (22-26)	32 (25-39)	20 (19-21)
Trout	44 (33-55)	34 (32-36)	41 (27-55)	22 (21-23)	57 (38-76)	20 (18-22)	58 (44-72)	41 (39-43)	47 (40-54)	30 (29-31)
Total salmonid	79 (70-88)	60 (58-62)	65 (58-72)	35 (33-37)	85 (72-98)	29 (26-32)	93 (85-101)	65 (63-67)	79 (73-85)	50 (49-51)
Minnow	53 (41-65)	11 (10-12)	41 (27-55)	27 (26-28)	41 (22-60)	52 (49-55)	62 (47-77)	25 (23-27)	49 (42-56)	24 (23-25)
Eel	43 (32-54)	8 (7-9)	63 (49-77)	11 (10-12)	30 (13-47)	6 (5-7)	21 (9-33)	3 (2-4)	41 (34-48)	7
Stoneloach	42 (31-53)	18 (17-19)	45 (31-59)	26 (25-27)	41 (22-60)	13 (11-15)	24 (11-37)	6 (5-7)	39 (32-46)	17 (16-18)
Stickleback	11 (4-18)	2	10 (2-18)	2	11 (-1-23)	0	8 (0-16)	1	10 (6-14)	2
Total fish	99 (97-101)	-	96 (91-101)	-	96 (89-103)	-	100	-	98 (96-100)	-
Mammal	11 (4-18)	-	4 (-1-9)	-	7 (-3-17)	-	8 (0-16)	-	8 (4-12)	-
Amphibian	13 (5-21)	-	0	-	0	-	8 (0-16)	-	7 (4-11)	-
Bird	0	-	2 (-2-6)	-	0	-	0	-	1 (0-2)	-
Invertebrate	0	-	0	-	0	-	0	-	0	-
n	72 spraints	3721 occurrences	49 spraints	3393 occurrences	27 spraints	1237 occurrences	42 spraints	2468 occurrences	190 spraints	10819 occurrences

Table VI.II Frequencies (f) and proportions (p) of salmonids in each size class calculated from the width of atlas bones found in otter spraints collected during four seasonal surveys of the upper Tyne catchment between 1993 and 1994. Corrected frequencies and proportions are also provided which take into account size-related differential recovery of atlas bones after Carss & Elston (1996).

Length class		Salmon atlas				Trout atlas				All atlas			
		Actual		Corrected		Actual		Corrected		Actual		Corrected	
class	length (mm)	f	p	f	p	f	p	f	p	f	p	f	p
1	≤30	1	0.04	3.5	0.05	2	0.05	6.9	0.08	3	0.05	10.4	0.07
2	>30≤40	3	0.11	9.4	0.15	2	0.05	6.1	0.07	6	0.09	18.6	0.12
3	>40≤50	1	0.04	2.9	0.05	0	0	0	0	1	0.02	2.9	0.02
4	>50≤60	3	0.11	8.1	0.13	3	0.08	7.9	0.09	6	0.09	16.0	0.11
5	>60≤70	4	0.15	9.7	0.15	9	0.23	21.8	0.25	13	0.20	31.4	0.21
6	>70≤80	6	0.22	13.5	0.21	5	0.13	11.2	0.13	10	0.15	22.5	0.15
7	>80≤90	2	0.07	4.3	0.07	5	0.13	10.7	0.12	7	0.11	15.0	0.10
8	>90≤100	4	0.15	7.7	0.12	3	0.08	5.9	0.07	7	0.11	13.6	0.09
9	>100≤110	1	0.04	1.8	0.03	1	0.03	1.8	0.02	2	0.03	3.6	0.02
10	>110≤120	0	0	0	0	1	0.03	1.7	0.02	1	0.02	1.7	0.01
11	>120≤130	2	0.07	3.3	0.05	1	0.03	1.6	0.02	3	0.05	4.9	0.03
12	>130≤140	0	0	0	0	3	0.08	4.7	0.05	3	0.05	4.7	0.03
13	>140≤150	0	0	0	0	2	0.05	3.0	0.03	2	0.03	3	0.02
14	>150≤160	0	0	0	0	0	0	0	0	0	0	0	0
15	>160≤170	0	0	0	0	1	0.03	1.3	0.02	1	0.02	1.3	0.009
16	>170	0	0	0	0	1	0.03	1.3	0.02	1	0.02	1.3	0.009
	n	27 atlas				39 atlas				66 atlas			

Table VI.III Frequencies (f) and proportions (p) of salmonids in each size class calculated from the length of caudal and thoracic vertebrae found in otter spraints collected during each of four seasonal surveys of the upper Tyne catchment between 1993 and 1994.

Length class		Caudal vertebrae								Thoracic vertebrae							
Class	Length	Spring 1993		Summer 1993		Autumn 1994		Winter 1994		Spring 1993		Summer 1993		Autumn 1994		Winter 1994	
	(mm)	f	p	f	p	f	p	f	p	f	p	f	p	f	p	f	p
1	≤40	1	0.001	13	0.02	0	0	0	0	0	0	0	0	0	0	2	0.003
2	>40≤50	41	0.05	183	0.33	5	0.03	72	0.12	1	0.001	116	0.23	1	0.007	28	0.04
3	>50≤60	108	0.13	47	0.08	9	0.06	92	0.15	79	0.08	69	0.14	13	0.09	114	0.17
4	>60≤70	313	0.38	114	0.20	49	0.33	212	0.35	248	0.26	70	0.14	15	0.10	154	0.23
5	>70≤80	101	0.12	46	0.08	25	0.17	44	0.07	363	0.38	149	0.29	51	0.35	191	0.28
6	>80≤90	88	0.11	27	0.05	4	0.03	28	0.05	54	0.06	41	0.08	9	0.06	51	0.08
7	>90≤100	58	0.07	69	0.12	10	0.07	34	0.06	83	0.09	24	0.05	10	0.07	45	0.07
8	>100≤110	13	0.02	21	0.04	17	0.12	21	0.03	51	0.05	28	0.05	23	0.16	26	0.04
9	>110≤120	23	0.03	27	0.05	5	0.03	6	0.01	25	0.03	8	0.02	4	0.03	24	0.04
10	>120≤130	41	0.05	6	0.01	14	0.10	47	0.08	14	0.01	2	0.004	10	0.07	11	0.02
11	>130≤140	9	0.01	1	0.002	1	0.007	23	0.04	6	0.006	3	0.005	5	0.03	18	0.03
12	>140≤150	14	0.02	3	0.005	5	0.03	18	0.03	2	0.002	0	0	1	0.007	4	0.006
13	>150≤160	4	0.005	2	0.004	1	0.007	6	0.01	10	0.01	0	0	1	0.007	2	0.003
14	>160≤170	6	0.007	0	0	0	0	1	0.001	6	0.006	0	0	1	0.007	4	0.006
15	>170≤180	3	0.004	0	0	0	0	4	0.007	3	0.003	0	0	1	0.007	0	0
16	>180≤190	0	0	0	0	0	0	2	0.003	3	0.003	0	0	0	0	0	0
17	>190≤200	0	0	0	0	0	0	2	0.003	2	0.002	0	0	0	0	0	0
18	>200	0	0	0	0	2	0.01	1	0.001	3	0.003	0	0	0	0	0	0
	n	823 vertebrae		559 vertebrae		147 vertebrae		613 vertebrae		950 vertebrae		510 vertebrae		145 vertebrae		674 vertebrae	

Table VI.IV Frequencies (f) and proportions (p) (with corrections for size-related differential recovery of thoracic vertebrae) of eels in each length class estimated from the lengths of thoracic vertebrae found in otter spraints collected during four seasonal surveys of the upper Tyne catchment between 1993 and 1994.

Length classes		Actual		Corrected	
Class	length (mm)	f	p	f	p
1	≤150	6	0.04	11.4	0.03
2	>150≤200	2	0.01	4.3	0.009
3	>200≤250	31	0.23	88.9	0.20
4	>250≤300	29	0.21	83.4	0.18
5	>300≤350	38	0.28	128.4	0.28
6	>350≤400	13	0.10	51.2	0.11
7	>400≤450	9	0.07	43.7	0.10
8	>450≤500	6	0.04	32.2	0.07
9	>500≤550	0	0	0	0
10	>550≤600	0	0	0	0
11	>600	1	0.007	10.3	0.02
	n	135 thoracic vertebrae			

Table VI.V Frequencies (f) and proportions (p) of minnows in each size class estimated from the 'gape' measurement of pharyngeal bones found in otter spraints collected during each of four seasonal surveys of the upper Tyne catchment between 1993 and 1994.

Length class		Spring		Summer		Autumn		Winter		Overall	
Class	Length (mm)	f	p	f	p	f	p	f	p	f	p
1	>20≤25	0	0	0	0	2	0.03	0	0	2	0.01
2	>25≤30	0	0	1	0.03	1	0.01	0	0	2	0.01
3	>30≤35	2	0.10	2	0.06	23	0.34	2	0.07	29	0.19
4	>35≤40	2	0.10	2	0.06	24	0.06	3	0.11	11	0.07
5	>40≤45	3	0.15	10	0.28	4	0.06	1	0.04	18	0.12
6	>45≤50	3	0.15	10	0.28	16	0.24	6	0.21	35	0.23
7	>50≤55	1	0.05	8	0.22	6	0.09	6	0.21	21	0.14
8	>55≤60	6	0.30	2	0.06	6	0.09	7	0.25	21	0.14
9	>60≤65	1	0.05	1	0.03	2	0.03	1	0.04	5	0.03
10	>65≤70	2	0.10	0	0	1	0.01	0	0	3	0.02
11	>70≤75	0	0	0	0	2	0.03	1	0.04	3	0.02
12	>75≤80	0	0	0	0	1	0.01	0	0	1	0.007
13	>80	0	0	0	0	0	0	1	0.04	1	0.007
	n	20 pharyngeal bones		36 pharyngeal bones		68 pharyngeal bones		28 pharyngeal bones		152 pharyngeal bones	

Table VI.VI Frequencies (f) and proportions (p) of all stoneloach in each size estimated from the lengths of caudal and thoracic vertebrae found in otter spraints collected from the upper Tyne between 1993 and 1994.

Length class		Caudal vertebrae		Thoracic vertebrae		All vertebrae	
Class	Length (mm)	f	p	f	p	f	p
1	≤30	12	0.02	11	0.01	23	0.01
2	>30≤40	40	0.05	72	0.06	112	0.06
3	>40≤50	109	0.14	92	0.08	201	0.11
4	>50≤60	134	0.17	166	0.15	300	0.16
5	>60≤70	86	0.11	196	0.18	282	0.15
6	>70≤80	132	0.17	212	0.19	344	0.18
7	>80≤90	151	0.19	176	0.16	327	0.17
8	>90≤100	82	0.10	131	0.12	213	0.11
9	>100≤110	31	0.04	39	0.04	70	0.04
10	>110	18	0.02	13	0.01	31	0.02
	n	795 vertebrae		1108 vertebrae		1903 vertebrae	

Table VI. VII: Frequencies (f) and proportions (p) of stoneloach in each size class estimated from the lengths of caudal and thoracic vertebrae found in otter spraints collected from the upper Tyne catchment in four seasonal surveys between 1993 and 1994.

Length class (mm)	Caudal								Thoracic							
	Spring		Summer		Autumn		Winter		Spring		Summer		Autumn		Winter	
	f	p	f	p	f	p	f	p	f	p	f	p	f	p	f	p
≤30	0	0	11	0.03	0	0	1	0.02	2	0.006	6	0.01	3	0.05	0	0
>30≤40	0	0	34	0.08	6	0.06	0	0	13	0.04	51	0.08	2	0.04	6	0.08
>40≤50	5	0.02	77	0.18	21	0.22	6	0.15	25	0.07	51	0.08	2	0.04	16	0.21
>50≤60	21	0.10	63	0.14	29	0.31	11	0.27	42	0.11	89	0.15	18	0.32	17	0.22
>60≤70	15	0.07	49	0.11	20	0.21	2	0.05	52	0.14	116	0.19	14	0.25	14	0.18
>70≤80	48	0.23	68	0.15	8	0.08	8	0.20	83	0.22	106	0.18	5	0.09	18	0.23
>80≤90	46	0.22	86	0.20	7	0.07	12	0.29	58	0.16	111	0.18	5	0.09	2	0.03
>90≤100	40	0.19	39	0.09	2	0.02	1	0.02	69	0.19	57	0.09	2	0.04	3	0.04
>100≤110	19	0.09	11	0.03	1	0.01	0	0	19	0.05	18	0.03	1	0.02	1	0.01
>110	16	0.08	1	0.002	1	0.01	0	0	8	0.03	0	0	5	0.09	0	0
n	210 vertebrae		439 vertebrae		95 vertebrae		41 vertebrae		371 vertebrae		605 vertebrae		57 vertebrae		77 vertebrae	

APPENDIX VII ELECTRO-FISHING RESULTS

Table VII. I Results of an electro-fishing survey of the upper Tyne catchment in the summer of 1995 showing population estimates and 95% Confidence Intervals for the five main species at each survey site. (For locations of sites see Figure 4.2.1)

Salmonids

Watercourse	Site code	Population estimates (number of fish per $100m^{2)}$					
		Salmon		Trout		All salmonid	
		Estimate	±95% C.I.	Estimate	±95% C.I.	Estimate	±95% C.I.
R. South Tyne	1	3	-	0	-	3	-
R. South Tyne	2	32	-	1	-	34	-
R. South Tyne	3	0	-	0	-	0	-
R. South Tyne	4	0	-	32	-	32	-
R. South Tyne	5	8	-	13	-	22	-
R. South Tyne	6	0	-	4	-	4	-
R. South Tyne	7	0	-	8	-	8	-
R. South Tyne	8	0	-	18	-	18	-
R. South Tyne	9	0	-	59	4	59	4
R. South Tyne	10	0	-	71	5	71	5
R. South Tyne	11	0	-	47	-	47	-
R. South Tyne	12	0	-	67	-	67	-
R. South Tyne	13	0	-	75	18	75	18
R. Allen	14	0	-	11	-	11	-
R. Allen	15	7	-	72	4	84	19
R. East Allen	16	36	-	202	7	233	11
R. East Allen	17	0	-	62	14	62	14
R. East Allen	18	0	-	30	-	30	-
R. East Allen	19	0	-	12	-	12	-
R. East Allen	20	0	-	62	7	62	7
R. East Allen	21	0	-	15	-	15	-
R. West Allen	22	0	-	10	-	10	-
R. West Allen	23	0	-	25	-	25	-
R. West Allen	24	0	-	8	-	8	-
R. West Allen	25	0	-	10	-	10	-
R. West Allen	26	0	-	0	-	0	-
Haltwhistle B.	27	0	-	120	13	120	13
Haltwhistle B.	28	0	-	47	-	47	-
Park B.	29	0	-	28	-	28	-
Park B.	30	0	-	71	3	71	3
Hartley B.	31	0	-	270	80	270	80
Hartley B.	32	0	-	298	24	298	24
Hartley B.	33	0	-	184	20	184	20
R. Nent	34	0	-	0	-	0	-
R. Nent	35	0	-	8	-	8	-
R. Nent	36	0	-	1	-	1	-
Black B.	37	0	-	116	50	116	50
Black B.	38	0	-	144	10	144	10
R. North Tyne	39	0	-	0	-	0	-
R. North Tyne	40	0	-	1	-	1	-
R. North Tyne	41	8	-	0	-	8	-
R. North Tyne	42	29	-	0	-	29	-
R. North Tyne	43	0	-	0	-	0	-
R. North Tyne	44	0	-	1	-	1	-
R. North Tyne	45	22	-	2	-	24	-
R. North Tyne	46	0	-	0	-	0	-
R. North Tyne	47	34	-	19	-	55	28
R. North Tyne	48	4	-	8	-	12	-
R. North Tyne	49	9	-	0	-	9	-
R. North Tyne	50	9	-	1	-	11	-

Table VII. I continued.

Watercourse	Site code	Population estimates (number of fish per $100m^{2)}$					
		Salmon		Trout		All salmonid	
		Estimate	±95% C.I.	Estimate	±95% C.I.	Estimate	±95% C.I.
R. North Tyne	51	0	-	9	-	9	-
R. North Tyne	52	0	-	0	-	0	-
Deadwater B.	53	0	-	109	16	109	16
Deadwater B.	54	0	-	8	-	8	-
Deadwater B.	55	6	-	3	-	3	-
Kielder B.	56	12	-	0	-	12	-
Kielder B.	57	12	-	1	-	14	-
Kielder B.	58	0	-	1	-	1	-
Kielder B.	59	0	-	0	-	0	-
Kielder B.	60	0	-	0	-	0	-
Kielder B.	61	0	-	0	-	0	-
Kielder B.	62	0	-	0	-	0	-
Kielder B.	63	0	-	1	-	1	-
Kielder B.	64	0	-	1	-	1	-
Scaup B.	65	0	-	1	-	1	-
Little Whickhope B.	66	0	-	0	-	0	-
Lewis B.	67	0	-	0	-	0	-
Lewis B.	68	0	-	3	-	3	-
Lewis B.	69	0	-	0	-	0	-
Tarset B.	70	1	-	19	-	22	-
Tarset B.	71	5	-	28	-	36	-
Tarset B.	72	0	-	42	-	42	-
Tarret B.	73	0	-	178	22	178	22
Tarret B.	74	0	-	273	17	273	17
Chirdon B.	75	0	-	35	-	35	-
Chirdon B.	76	0	-	0	-	0	-
R. Rede	77	45	-	7	-	52	6
R. Rede	78	1	-	0	-	1	-
R. Rede	79	0	-	0	-	0	-
R. Rede	80	26	-	6	-	32	-
R. Rede	81	2	-	1	-	4	-
R. Rede	82	14	-	4	-	18	-
R. Rede	83	8	-	0	-	8	-
R. Rede	84	30	-	4	-	34	-
R. Rede	85	482	12	130	24	616	48
R. Rede	86	11	-	9	-	21	-
R. Rede	87	1	-	10	-	12	-
Houxty B.	88	0	-	95	8	95	8
Houxty B.	89	2	-	38	-	42	-
Houxty B.	90	1	-	21	-	23	-
Warks B.	91	4	-	62	5	67	6
Warks B.	92	9	-	68	6	71	3
Warks B.	93	0	-	35	-	35	-
Swin B.	94	0	-	28	-	28	-
Swin B.	95	0	-	81	4	81	4
Erring B.	96	0	-	78	11	78	11
Erring B.	97	0	-	139	10	139	10

Table VII. I continued

Other species

Watercourse	Site code	Population estimates (number of fish per $100m^{2}$)					
		Eel		Minnow		Stonelaoch	
		Estimate	±95% C.I.	Estimate	±95% C.I.	Estimate	±95% C.I.
R. South Tyne	1	0	-	0	-	32	-
R. South Tyne	2	1	-	1	-	40	-
R. South Tyne	3	2	-	1	-	26	-
R. South Tyne	4	1	-	0	-	21	-
R. South Tyne	5	0	-	0	-	23	-
R. South Tyne	6	2	-	3	-	62	4
R. South Tyne	7	0	-	0	-	9	-
R. South Tyne	8	1	-	0	-	3	-
R. South Tyne	9	1	-	0	-	3	-
R. South Tyne	10	1	-	0	-	0	-
R. South Tyne	11	2	-	0	-	7	-
R. South Tyne	12	3	-	0	-	0	-
R. South Tyne	13	0	-	0	-	0	-
R. Allen	14	3	-	207	180	88	16
R. Allen	15	2	-	16	-	35	-
R. East Allen	16	0	-	0	-	53	11
R. East Allen	17	2	-	0	-	5	-
R. East Allen	18	0	-	0	-	15	-
R. East Allen	19	0	-	0	-	14	-
R. East Allen	20	2	-	0	-	0	-
R. East Allen	21	0	-	0	-	0	-
R. West Allen	22	4	-	0	-	0	-
R. West Allen	23	0	-	0	-	0	-
R. West Allen	24	0	-	0	-	0	-
R. West Allen	25	0	-	0	-	0	-
R. West Allen	26	0	-	0	-	0	-
Haltwhistle B.	27	8	-	122	-	22	-
Haltwhistle B.	28	1	-	23	-	53	11
Park B.	29	1	-	0	-	38	-
Park B.	30	0	-	0	-	0	-
Hartley B.	31	1	-	0	-	32	-
Hartley B.	32	0	-	0	-	24	-
Hartley B.	33	0	-	0	-	0	-
R. Nent	34	0	-	0	-	0	-
R. Nent	35	0	-	0	-	0	-
R. Nent	36	0	-	0	-	0	-
Black B.	37	0	-	0	-	0	-
Black B.	38	1	-	0	-	0	-
R. North Tyne	39	0	-	64	64	4	-
R. North Tyne	40	4	-	2	-	28	-
R. North Tyne	41	12	-	2	-	1	-
R. North Tyne	42	1	-	1	-	87	-
R. North Tyne	43	0	-	0	-	0	-
R. North Tyne	44	0	-	1	-	1	-
R. North Tyne	45	22	-	2	-	24	-
R. North Tyne	46	0	-	0	-	0	-
R. North Tyne	47	34	-	19	-	55	-
R. North Tyne	48	4	-	8	-	12	-
R. North Tyne	49	9	-	0	-	9	-
R. North Tyne	50	9	-	1	-	11	-

Table VII. I continued

Watercourse	Site code	Population estimates (number of fish per $100m^{-2}$)					
		Eel		Minnow		Stonelaoch	
		Estimate	±95% C.I.	Estimate	±95% C.I.	Estimate	±95% C.I.
R. North Tyne	51	2	-	3	-	1	-
R. North Tyne	52	5	-	69	20	0	-
Deadwater B.	53	1	-	41	-	25	-
Deadwater B.	54	0	-	171	93	130	7
Deadwater B.	55	1	-	4	-	94	20
Kielder B.	56	1	-	73	68	38	4
Kielder B.	57	0	-	175	317	39	-
Kielder B.	58	0	-	157	98	62	10
Kielder B.	59	0	-	57	60	27	-
Kielder B.	60	0	-	9	-	20	-
Kielder B.	61	0	-	23	-	12	-
Kielder B.	62	1	-	30	-	27	-
Kielder B.	63	0	-	11	-	65	41
Kielder B.	64	0	-	47	-	20	-
Scaup B.	65	0	-	85	-	9	-
Little Whickhope B.	66	0	-	165	55	8	-
Lewis B.	67	0	-	46	-	0	-
Lewis B.	68	0	-	10	-	0	-
Lewis B.	69	0	-	17	-	0	-
Tarset B.	70	8	-	19	-	0	-
Tarset B.	71	6	-	16	-	0	-
Tarset B.	72	0	-	17	-	0	-
Tarret B.	73	3	-	0	-	42	-
Tarret B.	74	1	-	0	-	0	-
Chirdon B.	75	2	-	0	-	0	-
Chirdon B.	76	0	-	0	-	0	-
R. Rede	77	7	-	52	26	45	-
R. Rede	78	4	-	18	-	100	15
R. Rede	79	0	-	37	-	26	-
R. Rede	80	8	-	72	-	87	15
R. Rede	81	3	-	46	-	52	27
R. Rede	82	16	-	157	96	16	-
R. Rede	83	6	-	83	51	28	-
R. Rede	84	6	-	23	-	9	-
R. Rede	85	0	-	33	-	9	-
R. Rede	86	3	-	29	-	0	-
R. Rede	87	0	-	10	-	3	-
Houxty B.	88	4	-	44	-	48	-
Houxty B.	89	5	-	14	-	17	-
Houxty B.	90	1	-	104	8	8	-
Warks B.	91	23	-	138	10	7	-
Warks B.	92	4	-	37	-	39	-
Warks B.	93	5	-	72	27	1	-
Swin B.	94	0	-	0	-	0	-
Swin B.	95	12	-	0	-	0	-
Erring B.	96	2	-	0	-	14	-
Erring B.	97	1	-	0	-	5	-

Stickleback, bullhead and lamprey were also caught during the survey but were present at only a few sites and in low numbers.

Table VII.II Frequencies (f) and proportions (p) of salmonids in each size class caught during an electro-fishing survey of the upper Tyne catchment between July and August 1995.

Size		salmon		trout		all salmonids	
Class	length (mm)	f	p	f	p	f	p
1	>30≤40	5	0.007	40	0.01	45	0.01
2	>40≤50	159	0.21	484	0.15	643	0.16
3	>50≤60	297	0.39	924	0.28	1221	0.30
4	>60≤70	86	0.11	489	0.15	575	0.14
5	>70≤80	14	0.02	157	0.05	171	0.04
6	>80≤90	13	0.02	107	0.03	120	0.03
7	>90≤100	36	0.05	152	0.05	188	0.05
8	>100≤110	75	0.10	202	0.06	277	0.07
9	>110≤120	51	0.07	199	0.06	250	0.06
10	>120≤130	21	0.03	158	0.05	179	0.04
11	>130≤140	3	0.004	106	0.03	109	0.03
12	>140≤150	1	0.001	57	0.02	58	0.01
13	>150≤160	1	0.001	42	0.01	43	0.01
14	>160≤170	0	0	28	0.009	28	0.007
15	>170≤180	0	0	29	0.009	29	0.007
16	>180≤190	0	0	21	0.006	21	0.005
17	>190≤200	0	0	11	0.003	11	0.003
18	>200≤250	0	0	30	0.009	30	0.007
19	>200≤250	0	0	9	0.003	9	0.002
	n	762 fish		3245 fish		4007 fish	

Table VII.III Frequencies (f) and proportions (p) of eels in each size class caught during an electro-fishing survey of the upper Tyne catchment between July and August 1995.

	Size		
Class	length (mm)	f	p
1	>100≤150	1	0.004
2	>150≤200	5	0.02
3	>200≤250	20	0.08
4	>250≤300	42	0.17
5	>300≤350	62	0.25
6	>350≤400	56	0.22
7	>400≤450	24	0.10
8	>450≤500	22	0.09
9	>500≤550	14	0.06
10	>550≤600	2	0.008
11	>600≤650	0	0
12	>650≤700	1	0.004
	n	249 fish	

Table VII.IV Frequencies (f) and proportions (p) of minnows caught during an electro-fishing survey of the upper Tyne catchment between July and August 1995.

	Size		
Class	length (mm)	f	p
1	>30≤35	8	0.004
2	>35≤40	67	0.03
3	>40≤45	195	0.10
4	>45≤50	333	0.17
5	>50≤55	378	0.19
6	>55≤60	416	0.21
7	>60≤65	251	0.13
8	>65≤70	162	0.08
9	>70≤75	100	0.05
10	>75≤80	51	0.03
11	>80≤85	15	0.008
12	>85≤90	8	0.004
13	>90≤95	0	0
14	>95≤100	0	0
15	>100≤155	7	0.004
	n	1991 fish	

Table VII.V Frequencies (f) and proportions (p) of stoneloach caught during an electro-fishing survey of the upper Tyne catchment between July and August 1995.

	Size		
Class	length (mm)	f	p
1	>30≤35	11	0.007
2	>35≤40	27	0.016
3	>40≤45	31	0.019
4	>45≤50	66	0.04
5	>50≤55	174	0.11
6	>55≤60	233	0.14
7	>60≤65	259	0.16
8	>65≤70	151	0.09
9	>70≤75	123	0.08
10	>75≤80	81	0.05
11	>80≤85	70	0.04
12	>85≤90	91	0.06
13	>90≤95	119	0.07
14	>95≤100	78	0.05
15	>100≤105	65	0.04
16	>105≤110	31	0.02
17	>110≤115	13	0.008
18	>115≤155	6	0.004
	n	1629 fish	

APPENDIX VIII SUMMARY STATISTICS FOR ALL ENVIRONMENTAL VARIABLES USED IN CHAPTER 5

Table VIII.Ia Mean numbers of 100m sections per 5km stretch in three depth classes in each of four surveys of the upper Tyne catchment between 1993 and 1995. Mean and standard error values are given for the overall sample, for the North and South Tyne separately and for stretches with no otter signs (Absent) and stretches with otter signs (Present). These values were calculated after back transformation from log-transformed variables. DEP1 ≤0.25m, DEP2 >0.25≤0.5m, DEP3 >0.5m

Season	Depth class	Mean (SE)				
		All stretches	South Tyne	North Tyne	Absent	Present
Spring	DEP1	9.2(0.2)	8.3(0.5)	9.8(0.3)	11.6(0.4)	7.5(0.3)
	DEP2	10.1(0.2)	8.1(0.4)	11.7	8.0(0.4)	12.2(0.2)
	DEP3	10.8(0.2)	10.0(0.4)	11.4(0.3)	8.2(0.4)	13.5(0.2)
Summer	DEP1	15.4(0.2)	18.8(0.2)	13.5(0.3)	16.9(0.3)	13.3(0.3)
	DEP2	11.5(0.2)	17.2(0.2)	8.7(0.3)	10.4(0.3)	13.7(0.2)
	DEP3	6.3(0.2)	4.1(0.3)	8.4(0.3)	4.4(0.3)	11.2(0.2)
Autumn	DEP1	7.2(0.2)	11.6(0.3)	5.1(0.3)	8.5(0.3)	5.7(0.3)
	DEP2	13.2(0.2)	16.6(0.3)	11.3(0.3)	7.9(0.3)	18.8(0.2)
	DEP3	11.5	6.2(0.4)	17.0(0.2)	7.9(0.3)	18.9(0.2)
Winter	DEP1	6.2(0.2)	10.1(0.3)	4.4(0.3)	5.6(0.3)	7.6(0.4)
	DEP2	12.9(0.2)	20.0(0.2)	9.6(0.3)	12.7(0.3)	13.5(0.2)
	DEP3	9.8(0.2)	6.9(0.3)	12.2(0.4)	7.0(0.3)	20.4(0.2)

Table VIII.Ib Percentages of 2.5km stretches in four depth classes in each of four surveys of the upper Tyne catchment between 1993 and 1995. Values are given for the overall sample, for the North and South Tyne separately and for stretches with no otter signs (Absent) and stretches with otter signs (Present). DEP1 ≤0.25m, DEP2 >0.25≤0.5m, DEP3 >0.5m≤1m, DEP4 >1m

Season	Depth class	Percentage of stretches % (n)				
		All stretches	South Tyne	North Tyne	Absent	Present
Spring	DEP1	21(15)	29(8)	17(7)	22(8)	21(7)
	DEP2	43(30)	39(11)	45(19)	45(17)	39(13)
	DEP3	21(15)	21(6)	21(9)	11(4)	33(11)
	DEP4	15(10)	11(3)	17(7)	22(8)	6(2)
Summer	DEP1	40(28)	29(8)	48(20)	44(20)	32(8)
	DEP2	41(29)	68(19)	24(10)	38(17)	48(12)
	DEP3	6(4)	4(1)	7(3)	4(2)	8(2)
	DEP4	13(9)	0(0)	21(9)	13(6)	12(3)
Autumn	DEP1	20(14)	21(6)	19(8)	25(13)	6(1)
	DEP2	49(34)	61(17)	40(17)	54(28)	33(6)
	DEP3	16(11)	7(2)	21(9)	8(4)	39(7)
	DEP4	16(11)	11(3)	19(8)	13(7)	22(4)
Winter	DEP1	14(10)	11(3)	17(7)	17(8)	14(3)
	DEP2	51(36)	71(20)	38(16)	54(26)	41(9)
	DEP3	21(15)	18(5)	24(10)	15(7)	36(8)
	DEP4	13(9)	0(0)	19(9)	15(7)	9(2)

Table VIII.Ic Percentages of 1km stretches in four depth classes in each of four surveys of the upper Tyne catchment between 1993 and 1995. Values are given for the overall sample, for the North and South Tyne separately and for stretches with no otter signs (Absent) and stretches with otter signs (Present). DEP1 ≤0.25m, DEP2 >0.25≤0.5m, DEP3 >0.5m≤1m, DEP4 >1m.

Season	Depth class	Percentage of stretches % (n)				
		All stretches	South Tyne	North Tyne	Absent	Present
Spring	DEP1	31(56)	27(20)	33(36)	30(38)	32(18)
	DEP2	32(58)	37(27)	28(31)	35(44)	25(14)
	DEP3	0(0)	0(0)	0(0)	0(0)	0(0)
	DEP4	37(68)	36(26)	39(42)	34(43)	44(25)
Summer	DEP1	38(70)	38(28)	38(42)	41(54)	35(17)
	DEP2	37(68)	48(35)	30(33)	35(47)	41(20)
	DEP3	10(19)	8(6)	12(13)	7(9)	20(10)
	DEP4	14(25)	5(4)	19(21)	17(23)	8(2)
Autumn	DEP1	20(37)	23(17)	18(20)	24(35)	8(3)
	DEP2	46(83)	58(42)	38(41)	50(72)	26(10)
	DEP3	19(35)	10(7)	26(28)	12(17)	47(18)
	DEP4	15(27)	10(7)	18(20)	14(20)	18(7)
Winter	DEP1	21(38)	16(12)	24(26)	23(29)	20(11)
	DEP2	41(74)	63(46)	26(28)	43(54)	34(19)
	DEP3	25(45)	18(13)	29(32)	17(22)	39(22)
	DEP4	14(25)	3(2)	21(23)	17(21)	7(4)

Table VIII.Id Percentages of 600m stretches in four depth classes in each of four surveys of the upper Tyne catchment between 1993 and 1995. Values are given for the overall sample, for the North and South Tyne separately and for stretches with no otter signs (Absent) and stretches with otter signs (Present). DEP1 ≤0.25m, DEP2 >0.25≤0.5m, DEP3 >0.5m≤1m, DEP4 >1m.

Season	Depth class	Percentage of stretches % (n)				
		All stretches	South Tyne	North Tyne	Absent	Present
Spring	DEP1	29(87)	32(38)	27(49)	29(66)	28(22)
	DEP2	37(112)	34(41)	39(71)	38(85)	33(26)
	DEP3	17(53)	20(24)	16(29)	16(35)	23(18)
	DEP4	17(52)	14(17)	19(35)	17(38)	18(14)
Summer	DEP1	39(118)	41(49)	38(69)	43(104)	25(15)
	DEP2	39(118)	49(59)	32(59)	36(89)	47(28)
	DEP3	9(27)	6(7)	11(20)	6(15)	20(12)
	DEP4	13(41)	4(5)	20(36)	15(36)	8(5)
Autumn	DEP1	22(67)	31(37)	16(30)	25(64)	11(5)
	DEP2	44(135)	44(53)	45(82)	46(120)	29(13)
	DEP3	18(55)	14(17)	21(38)	15(38)	38(17)
	DEP4	15(47)	11(13)	18(34)	14(37)	22(10)
Winter	DEP1	19(58)	24(29)	16(29)	22(51)	12(8)
	DEP2	44(133)	54(65)	37(68)	45(107)	37(25)
	DEP3	23(70)	20(24)	25(46)	18(43)	40(27)
	DEP4	14(43)	2(2)	22(41)	15(35)	12(8)

Table VIII.Ie Percentages of 200m stretches in three depth classes in each of four surveys of the upper Tyne catchment between 1993 and 1995. Values are given for the overall sample, for the North and South Tyne separately and for stretches with no otter signs (Absent) and stretches with otter signs (Present). DEP1 ≤0.5m, DEP2 >0.5≤1m, DEP3 >1m

Season	Depth class	Percentage of stretches % (n)				
		All stretches	South Tyne	North Tyne	Absent	Present
Spring	DEP1	56(279)	54(104)	58(175)	57(205)	51(71)
	DEP2	24(121)	27(52)	15(47)	23(84)	26(37)
	DEP3	20(98)	20(38)	22(66)	19(68)	21(30)
Summer	DEP1	72(358)	86(167)	63(191)	72(285)	72(72)
	DEP2	13(64)	9(17)	15(47)	12(47)	17(17)
	DEP3	15(76)	5(10)	22(66)	16(65)	11(11)
Autumn	DEP1	55(272)	65(127)	48(145)	56(242)	44(29)
	DEP2	27(133)	21(69)	31(93)	26(113)	30(20)
	DEP3	19(93)	14(27)	22(66)	18(76)	26(17)
Winter	DEP1	54(268)	68(132)	45(136)	58(223)	40(45)
	DEP2	29(143)	26(51)	30(92)	25(97)	41(46)
	DEP3	17(87)	6(11)	25(76)	17(66)	19(21)

Table VIII.IIa Percentages of 5km stretches in two width classes in each of four surveys of the upper Tyne catchment between 1993 and 1995. Values are given for the overall sample, for the North and South Tyne separately and for stretches with no otter signs (Absent) and stretches with otter signs (Present). WID1 ≤ 10m, WID2 >10m.

Season	Width class	Percentage of stretches % (n)				
		All stretches	South Tyne	North Tyne	Absent	Present
Spring	WID1	55(22)	63(10)	50(12)	78(14)	36(8)
	WID2	45(18)	37(6)	50(12)	22(4)	64(14)
Summer	WID1	53(21)	50(8)	54(13)	64(16)	33(5)
	WID2	47(19)	50(8)	46(11)	36(9)	67(10)
Autumn	WID1	50(20)	63(10)	42(10)	65(15)	29(5)
	WID2	50(20)	37(6)	58(14)	35(8)	71(12)
Winter	WID1	47(19)	44(7)	50(12)	57(16)	25(3)
	WID2	53(21)	56(9)	50(12)	43(12)	75(9)

Table VIII.IIb Percentages of 2.5km stretches in four width classes in each of four surveys of the upper Tyne catchment between 1993 and 1995. Values are given for the overall sample, for the North and South Tyne separately and for stretches with no otter signs (Absent) and stretches with otter signs (Present). WID1 ≤5m, WID2 >5≤10m, WID3, >10≤30m, WID4 >30

Season	Width class	Percentage of stretches % (n)				
		All stretches	South Tyne	North Tyne	Absent	Present
Spring	WID1	17(12)	14(4)	19(8)	30(11)	3(1)
	WID2	34(24)	39(11)	31(13)	35(13)	33(11)
	WID3	29(20)	39(11)	21(9)	14(5)	45(15)
	WID4	20(14)	7(2)	33(14)	22(8)	18(6)
Summer	WID1	19(13)	14(4)	21(9)	29(13)	0(0)
	WID2	31(22)	32(9)	31(13)	36(16)	24(6)
	WID3	24(17)	36(10)	17(7)	20(9)	32(8)
	WID4	26(18)	18(5)	31(13)	16(7)	44(11)
Autumn	WID1	13(9)	7(2)	17(7)	15(8)	6(1)
	WID2	33(23)	39(11)	29(12)	37(19)	22(4)
	WID3	29(20)	39(11)	21(9)	31(16)	22(4)
	WID4	26(18)	4(14)	33(14)	17(9)	50(9)
Winter	WID1	16(11)	11(3)	19(8)	21(10)	5(1)
	WID2	29(20)	36(10)	24(10)	33(16)	18(4)
	WID3	31(22)	43(12)	24(10)	27(13)	41(9)
	WID4	24(17)	11(3)	33(14)	19(9)	36(8)

Table VIII.IIc Percentages of 1km stretches in five width classes in each of four surveys of the upper Tyne catchment between 1993 and 1995. Values are given for the overall sample, for the North and South Tyne separately and for stretches with no otter signs (Absent) and stretches with otter signs (Present). WID1 ≤5m, WID2 >5≤10m, WID3, >10≤20m, WID4 >10≤30m, WID5 >30m

Season	Width class	Percentage of stretches % (n)				
		All stretches	South Tyne	North Tyne	Absent	Present
Spring	WID1	16(29)	14(10)	17(19)	21(26)	7(4)
	WID2	32(58)	42(31)	25(27)	36(45)	21(12)
	WID3	20(36)	23(17)	17(19)	15(19)	30(17)
	WID4	10(18)	12(9)	8(9)	6(8)	18(10)
	WID5	23(41)	8(6)	32(35)	22(27)	25(14)
Summer	WID1	15(28)	10(7)	19(21)	19(25)	6(3)
	WID2	27(49)	36(26)	21(23)	31(41)	16(8)
	WID3	21(39)	22(16)	21(23)	22(29)	20(10)
	WID4	12(22)	18(13)	8(9)	10(13)	18(9)
	WID5	24(44)	15(11)	30(33)	19(25)	39(19)
Autumn	WID1	16(29)	12(9)	18(20)	17(25)	11(4)
	WID2	26(47)	37(27)	18(20)	28(41)	16(6)
	WID3	20(36)	14(10)	24(26)	23(33)	8(3)
	WID4	13(24)	25(18)	6(6)	12(17)	18(7)
	WID5	25(46)	12(9)	34(37)	19(28)	47(18)
Winter	WID1	14(25)	14(25)	16(17)	17(21)	7(4)
	WID2	32(58)	32(58)	29(32)	40(51)	13(7)
	WID3	20(36)	20(36)	17(18)	18(23)	23(13)
	WID4	13(24)	9(17)	6(6)	3(4)	23(13)
	WID5	25(46)	25(46)	39(36)	21(27)	34(19)

Table VIII.IId Percentages of 600m stretches in five width classes in each of four surveys of the upper Tyne catchment between 1993 and 1995. Values are given for the overall sample, for the North and South Tyne separately and for stretches with no otter signs (Absent) and stretches with otter signs (Present). WID1 ≤5m, WID2 >5≤10m, WID3, >10≤20m, WID4 >10≤30m, WID5 >30m

Season	Width class	Percentage of stretches % (n)				
		All stretches	South Tyne	North Tyne	Absent	Present
Spring	WID1	19(57)	18(21)	20(36)	25(55)	3(2)
	WID2	28(84)	36(43)	22(41)	30(67)	21(17)
	WID3	22(68)	26(31)	20(37)	18(41)	34(27)
	WID4	10(31)	12(14)	9(17)	8(18)	16(13)
	WID5	21(64)	9(11)	29(53)	19(43)	26(21)
Summer	WID1	18(54)	13(16)	21(38)	20(50)	7(4)
	WID2	28(85)	38(32)	26(47)	30(72)	22(13)
	WID3	18(56)	23(28)	15(28)	19(47)	15(9)
	WID4	13(38)	18(21)	9(17)	11(27)	18(11)
	WID5	23(71)	14(17)	29(54)	20(48)	38(23)
Autumn	WID1	18(55)	16(19)	20(36)	20(53)	7(3)
	WID2	21(64)	30(36)	15(28)	22(57)	13(6)
	WID3	24(74)	21(25)	27(49)	26(67)	16(7)
	WID4	12(35)	20(24)	6(11)	11(29)	13(6)
	WID5	25(76)	13(16)	33(60)	20(53)	51(23)
Winter	WID1	15(46)	13(15)	17(31)	18(43)	6(4)
	WID2	28(84)	32(38)	25(46)	33(77)	8(6)
	WID3	24(72)	28(33)	21(39)	23(54)	26(18)
	WID4	9(27)	13(16)	6(11)	6(14)	19(13)
	WID5	25(75)	15(18)	31(57)	20(48)	40(27)

Table VIII.IIe Percentages of 200m stretches in five width classes in each of four surveys of the upper Tyne catchment between 1993 and 1995. Values are given for the overall sample, for the North and South Tyne separately and for stretches with no otter signs (Absent) and stretches with otter signs (Present). WID1 ≤5m, WID2 >5≤10m, WID3, >10≤20m, WID4 >10≤30m, WID5 >30m.

Season	Width class	Percentage of stretches % (n)				
		All stretches	South Tyne	North Tyne	Absent	Present
Spring	WID1	15(73)	15(29)	14(44)	19(69)	4(4)
	WID2	22(109)	24(47)	20(62)	23(83)	25(26)
	WID3	24(121)	35(67)	18(54)	20(73)	46(48)
	WID4	15(74)	17(33)	13(41)	11(41)	32(33)
	WID5	24(121)	9(18)	34(103)	26(92)	28(29)
Summer	WID1	14(70)	11(21)	16(49)	16(62)	8(8)
	WID2	23(117)	25(49)	22(68)	24(96)	21(21)
	WID3	20(102)	23(42)	20(60)	19(77)	25(25)
	WID4	16(78)	25(48)	10(30)	15(61)	17(17)
	WID5	26(131)	18(34)	32(97)	26(102)	29(29)
Autumn	WID1	13(64)	10(19)	15(45)	13(55)	14(9)
	WID2	21(105)	27(53)	17(52)	22(94)	17(11)
	WID3	21(106)	22(42)	21(64)	23(99)	11(7)
	WID4	14(72)	28(45)	9(27)	14(59)	20(13)
	WID5	30(151)	18(35)	38(116)	29(124)	39(26)
Winter	WID1	10(50)	8(15)	12(35)	12(46)	2(2)
	WID2	25(123)	27(53)	23(70)	29(111)	11(12)
	WID3	25(125)	34(65)	33(100)	24(94)	28(31)
	WID4	12(60)	16(31)	10(29)	10(37)	21(23)
	WID5	28(140)	15(30)	36(110)	25(96)	39(44)

Table VIII.IIIa Mean numbers of 100m sections per 5km stretch in four substrate classes in each of four surveys of the upper Tyne catchment between 1993 and 1995. Mean and standard error values are given for the overall sample, for the North and South Tyne separately and for stretches with no otter signs (Absent) and stretches with otter signs (Present). These values were calculated after back transformation from log-transformed variables. SUB1 - stones <50mm diameter; SUB - stones <50mm (50%) stones >50mm < 250mm (50%); SUB3 - stones >50mm < 250mm; SUB4 - substantial boulders and bedrock.

Season	Substrate class	Mean (SE)				
		All stretches	South Tyne	North Tyne	Absent	Present
All	SUB1	5.7(0.2)	5.2(0.3)	6.2(0.4)	-	-
	SUB2	11.6(0.2)	19.7(0.2)	8.1(0.3)	-	-
	SUB3	4.3(0.2)	5.4(0.3)	3.6(0.3)	-	-
	SUB4	4.1(0.2)	6.7(0.3)	2.9(0.3)	-	-
Spring	SUB1	-	-	-	5.2(0.4)	6.2(0.3)
	SUB2	-	-	-	8.1(0.4)	15.5(0.1)
	SUB3	-	-	-	2.0(0.3)	7.3(0.3)
	SUB4	-	-	-	3.4(0.3)	4.8(0.2)
Summer	SUB1	-	-	-	5.5(0.3)	6.1(0.4)
	SUB2	-	-	-	9.1(0.3)	17.3(0.2)
	SUB3	-	-	-	3.0(0.3)	7.2(0.3)
	SUB4	-	-	-	4.6(0.3)	3.4(0.3)
Autumn	SUB1	-	-	-	4.8(0.4)	7.2(0.3)
	SUB2	-	-	-	8.4(0.3)	17.9(0.1)
	SUB3	-	-	-	3.4(0.3)	5.8(0.3)
	SUB4	-	-	-	4.5(0.3)	3.6(0.3)
Winter	SUB1	-	-	-	5.3(0.3)	6.8(0.4)
	SUB2	-	-	-	10.1(0.3)	16.1(0.2)
	SUB3	-	-	-	3.3(0.3)	7.4(0.4)
	SUB4	-	-	-	4.4(0.2)	3.4(0.4)

TableVIII.IIIb Percentages of 2.5km stretches in three substrate classes in each of four surveys of the upper Tyne catchment between 1993 and 1995. Values are given for the overall sample, for the North and South Tyne separately and for stretches with no otter signs (Absent) and stretches with otter signs (Present). SUB1 - stones <50mm diameter; SUB - stones <50mm (50%) stones >50mm < 250mm (50%); SUB3 - stones >50mm < 250mm.

Season	Substrate class	Percentage of stretches % (n)				
		All stretches	South Tyne	North Tyne	Absent	Present
All	SUB1	29(17)	26(6)	31(11)	-	-
	SUB2	50(29)	57(13)	46(16)	-	-
	SUB3	21(12)	17(4)	23(8)	-	-
Spring	SUB1	-	-	-	24(7)	34(10)
	SUB2	-	-	-	59(17)	41(12)
	SUB3	-	-	-	17(5)	24(7)
Summer	SUB1	-	-	-	29(10)	30(7)
	SUB2	-	-	-	51(18)	48(11)
	SUB3	-	-	-	20(7)	22(5)
Autumn	SUB1	-	-	-	29(12)	31(5)
	SUB2	-	-	-	55(23)	38(6)
	SUB3	-	-	-	17(7)	31(5)
Winter	SUB1	-	-	-	29(11)	30(6)
	SUB2	-	-	-	55(21)	40(8)
	SUB3	-	-	-	16(6)	30(6)

Table VIII.IIIc Percentages of 1km stretches in four substrate classes in each of four surveys of the upper Tyne catchment between 1993 and 1995. Values are given for the overall sample, for the North and South Tyne separately and for stretches with no otter signs (Absent) and stretches with otter signs (Present). SUB1 - stones <50mm diameter; SUB - stones <50mm (50%) stones >50mm < 250mm (50%); SUB3 - stones >50mm < 250mm; SUB4 - substantial boulders and bedrock.

Season	Substrate class	Percentage of stretches % (n)				
		All stretches	South Tyne	North Tyne	Absent	Present
All	SUB1	29(47)	17(12)	38(35)	-	-
	SUB2	40(65)	49(35)	33(30)	-	-
	SUB3	19(31)	17(12)	21(19)	-	-
	SUB4	13(21)	18(13)	9(8)	-	-
Spring	SUB1	-	-	-	31(33)	25(14)
	SUB2	-	-	-	39(42)	40(23)
	SUB3	-	-	-	19(20)	19(11)
	SUB4	-	-	-	11(12)	16(9)
Summer	SUB1	-	-	-	31(36)	22(11)
	SUB2	-	-	-	40(46)	39(19)
	SUB3	-	-	-	15(17)	29(14)
	SUB4	-	-	-	14(16)	10(5)
Autumn	SUB1	-	-	-	30(38)	24(9)
	SUB2	-	-	-	40(50)	39(15)
	SUB3	-	-	-	17(21)	26(10)
	SUB4	-	-	-	13(17)	11(4)
Winter	SUB1	-	-	-	30(32)	27(15)
	SUB2	-	-	-	38(41)	43(24)
	SUB3	-	-	-	19(20)	20(11)
	SUB4	-	-	-	14(15)	11(6)

Table VIII.IIId Percentages of 600m stretches in four substrate classes in each of four surveys of the upper Tyne catchment between 1993 and 1995. Values are given for the overall sample, for the North and South Tyne separately and for stretches with no otter signs (Absent) and stretches with otter signs (Present). SUB1 - stones <50mm diameter; SUB - stones <50mm (50%) stones >50mm < 250mm (50%); SUB3 - stones >50mm < 250mm; SUB4 - substantial boulders and bedrock.

Season	Substrate class	Percentage of stretches % (n)				
		All stretches	South Tyne	North Tyne	Absent	Present
All	SUB1	31(83)	18(22)	40(61)	-	-
	SUB2	37(101)	45(54)	31(47)	-	-
	SUB3	18(48)	16(19)	19(29)	-	-
	SUB4	15(40)	20(24)	10(16)	-	-
Spring	SUB1	-	-	-	34(66)	22(17)
	SUB2	-	-	-	37(72)	37(29)
	SUB3	-	-	-	15(28)	25(20)
	SUB4	-	-	-	14(27)	16(13)
Summer	SUB1	-	-	-	33(70)	22(13)
	SUB2	-	-	-	38(81)	33(20)
	SUB3	-	-	-	13(28)	33(20)
	SUB4	-	-	-	16(33)	12(7)
Autumn	SUB1	-	-	-	32(72)	24(11)
	SUB2	-	-	-	37(85)	36(16)
	SUB3	-	-	-	16(36)	27(12)
	SUB4	-	-	-	15(34)	13(6)
Winter	SUB1	-	-	-	33(68)	23(15)
	SUB2	-	-	-	34(70)	48(31)
	SUB3	-	-	-	16(34)	22(14)
	SUB4	-	-	-	17(35)	8(5)

Table VIII.IIIe Percentages of 200m stretches in four substrate classes in each of four surveys of the upper Tyne catchment between 1993 and 1995. Values are given for the overall sample, for the North and South Tyne separately and for stretches with no otter signs (Absent) and stretches with otter signs (Present). SUB1 - stones <50mm diameter; SUB - stones <50mm (50%) stones >50mm < 250mm (50%); SUB3 - stones >50mm < 250mm; SUB4 - substantial boulders and bedrock.

Season	Substrate class	Percentage of stretches % (n)				
		All stretches	South Tyne	North Tyne	Absent	Present
All	SUB1	24(109)	18(35)	29(74)	-	-
	SUB2	38(169)	43(82)	34(87)	-	-
	SUB3	23(101)	18(34)	26(67)	-	-
	SUB4	15(68)	21(39)	11(29)	-	-
Spring	SUB1	-	-	-	26(83)	19(26)
	SUB2	-	-	-	40(123)	33(46)
	SUB3	-	-	-	20(63)	28(38)
	SUB4	-	-	-	13(40)	20(28)
Summer	SUB1	-	-	-	27(94)	15(15)
	SUB2	-	-	-	39(135)	34(34)
	SUB3	-	-	-	20(70)	31(31)
	SUB4	-	-	-	14(49)	19(19)
Autumn	SUB1	-	-	-	25(96)	21(13
	SUB2	-	-	-	39(148)	33(21)
	SUB3	-	-	-	20(78)	37(23)
	SUB4	-	-	-	16(62)	10(6)
Winter	SUB1	-	-	-	24(81)	26(28)
	SUB2	-	-	-	38(130)	36(39)
	SUB3	-	-	-	20(69)	30(32)
	SUB4	-	-	-	18(60)	7(8)

Table VIII.IVa Mean altitude (in metres above sea level) of 5km stretches in the upper Tyne catchment between 1993 and 1995. Mean and standard error values are given for the overall sample, for the North and South Tyne separately and for stretches with no otter signs (Absent) and stretches with otter signs (Present) in four different seasons. These values were calculated after back transformation from log-transformed variables.

Season	Mean (SE)				
	All stretches	South Tyne	North Tyne		
				Absent	Present
All	249(0.1)	293(0.1)	223(0.1)	-	-
Spring	-	-	-	302(0.1)	212(0.1)
Summer	-	-	-	312(0.1)	171(0.1)
Autumn	-	-	-	310(0.1)	184(0.1)
Winter	-	-	-	296(0.1)	165(0.1)

Table VIII.IVb Percentages of 2.5km stretches in two altitude classes in the upper Tyne catchment between 1993 and 1995. Values are given for the overall sample, for the North and South Tyne separately and for stretches with no otter signs (Absent) and stretches with otter signs (Present) in four seasons. ALT1 >100≤200m; ALT2 >200m.

Season	Altitude class	Percentage of stretches % (n)				
		All stretches	South Tyne	North Tyne	Absent	Present
All	ALT1	40(28)	29(8)	48(20)	-	-
	ALT2	60(42)	71(20)	52(22)	-	-
Spring	ALT1	-	-	-	70(26)	36(12)
	ALT2	-	-	-	30(11)	64(21)
Summer	ALT1	-	-	-	69(31)	28(7)
	ALT2	-	-	-	31(14)	72(18)
Autumn	ALT1	-	-	-	65(34)	22(4)
	ALT2	-	-	-	35(18)	78(14)
Winter	ALT1	-	-	-	71(34)	18(4)
	ALT2	-	-	-	29(14)	82(18)

Table VIII.IVc Percentages of 1km stretches in four altitude classes in the upper Tyne catchment between 1993 and 1995. Values are given for the overall sample, for the North and South Tyne separately and for stretches with no otter signs (Absent) and stretches with otter signs (Present) in four seasons. ALT1 >50≤150m; ALT2 >150≤225m; ALT3 >225≤300m; ALT4 >300m

Season	Altitude class	Percentage of stretches % (n)				
		All stretches	South Tyne	North Tyne	Absent	Present
All	ALT1	15(27)	14(10)	16(17)	-	-
	ALT2	27(49)	19(14)	32(35)	-	-
	ALT3	29(52)	23(17)	32(35)	-	-
	ALT4	30(54)	44(32)	22(20)	-	-
Spring	ALT1	-	-	-	10(13)	25(14)
	ALT2	-	-	-	22(28)	37(21)
	ALT3	-	-	-	34(42)	18(10)
	ALT4	-	-	-	34(42)	21(12)
Summer	ALT1	-	-	-	8(11)	33(16)
	ALT2	-	-	-	20(26)	47(23)
	ALT3	-	-	-	35(47)	10(5)
	ALT4	-	-	-	37(49)	10(5)
Autumn	ALT1	-	-	-	8(11)	42(16)
	ALT2	-	-	-	24(35)	37(14)
	ALT3	-	-	-	33(47)	13(5)
	ALT4	-	-	-	35(51)	8(3)
Winter	ALT1	-	-	-	9(11)	29(16)
	ALT2	-	-	-	22(28)	38(21)
	ALT3	-	-	-	34(43)	16(9)
	ALT4	-	-	-	35(44)	18(10)

TableVIII.IVd Percentages of 600m stretches in five altitude classes in the upper Tyne catchment between 1993 and 1995. Values are given for the overall sample, for the North and South Tyne separately and for stretches with no otter signs (Absent) and stretches with otter signs (Present) in four seasons. ALT1 >50≤150m; ALT2 >150≤200m; ALT3 >200≤300m; ALT4 >300≤400m; ALT5 >400m.

Season	Altitude class	Percentage of stretches % (n)				
		All stretches	South Tyne	North Tyne	Absent	Present
All	ALT1	15(45)	14(17)	15(28)	-	-
	ALT2	25(75)	17(20)	30(55)	-	-
	ALT3	30(91)	24(29)	34(62)	-	-
	ALT4	21(63)	21(25)	21(38)		
	ALT5	10(30)	24(29)	1(1)	-	-
Spring	ALT1	-	-	-	10(22)	29(23)
	ALT2	-	-	-	22(49)	33(26)
	ALT3	-	-	-	33(74)	21(17)
	ALT4				22(49)	18(14)
	ALT5	-	-	-	13(30)	0(0)
Summer	ALT1	-	-	-	10(24)	35(21)
	ALT2	-	-	-	19(47)	47(28)
	ALT3	-	-	-	35(85)	10(6)
	ALT4				24(58)	8(5)
	ALT5	-	-	-	12(30)	0(0)
Autumn	ALT1	-	-	-	11(28)	38(17)
	ALT2	-	-	-	21(55)	44(20)
	ALT3	-	-	-	33(86)	11(5)
	ALT4				23(60)	7(3)
	ALT5	-	-	-	12(30)	0(0)
Winter	ALT1	-	-	-	11(25)	29(20)
	ALT2	-	-	-	21(49)	38(26)
	ALT3	-	-	-	33(78)	19(13)
	ALT4				23(54)	13(9)
	ALT5	-	-	-	13(30)	0(0)

Table VIII.IVe Percentages of 200m stretches in five altitude classes in the upper Tyne catchment between 1993 and 1995. Values are given for the overall sample, for the North and South Tyne separately and for stretches with no otter signs (Absent) and stretches with otter signs (Present) in four seasons. ALT1 >50≤150m; ALT2 >150≤200m; ALT3 >200≤300m; ALT4 >300≤400m; ALT5 >400m.

Season	Altitude class	Percentage of stretches % (n)				
		All stretches	South Tyne	North Tyne	Absent	Present
All	ALT1	21(104)	21(40)	21(64)	-	-
	ALT2	29(142)	17(33)	36(109)	-	-
	ALT3	26(131)	25(48)	27(83)	-	-
	ALT4	16(81)	18(34)	15(47)		
	ALT5	8(40)	20(39)	<1(1)	-	-
Spring	ALT1	-	-	-	17(61)	31(43)
	ALT2	-	-	-	25(91)	36(51)
	ALT3	-	-	-	30(106)	18(25)
	ALT4				17(60)	15(21)
	ALT5	-	-	-	11(40)	0(0)
Summer	ALT1	-	-	-	18(70)	34(34)
	ALT2	-	-	-	25(100)	42(42)
	ALT3	-	-	-	29(116)	15(15)
	ALT4				18(72)	9(9)
	ALT5	-	-	-	10(40)	0(0)
Autumn	ALT1	-	-	-	19(80)	36(24)
	ALT2	-	-	-	26(114)	42(28)
	ALT3	-	-	-	28(120)	17(11)
	ALT4				18(78)	5(3)
	ALT5	-	-	-	9(40)	0(0)
Winter	ALT1	-	-	-	17(64)	36(40)
	ALT2	-	-	-	26(101)	37(41)
	ALT3	-	-	-	29(111)	18(20)
	ALT4				18(70)	10(11)
	ALT5	-	-	-	10(40)	0(0)

Table VIII.V Percentages of 5km, 2.5km, 1km, 600m and 200m stretches of riverbank with potential holt sites in the upper Tyne catchment between 1993 and 1995. Values are given for the overall sample, for the North and South Tyne separately and for stretches with no otter signs (Absent) and stretches with otter signs (Present) in four seasons.

Sample unit size	Season	Percentage of stretches % (n)				
		All stretches	South Tyne	North Tyne	Absent	Present
5km	All	65(40)	81(13)	54(13)	-	-
	Spring	-	-	-	44(8)	82(18)
	Summer	-	-	-	60(15)	73(11)
	Autumn	-	-	-	57(13)	76(13)
	Winter	-	-	-	57(16)	83(10)
2.5km	All	53(37)	75(21)	38(16)	-	-
	Spring	-	-	-	32(12)	76(25)
	Summer	-	-	-	42(19)	72(18)
	Autumn	-	-	-	44(23)	78(14)
	Winter	-	-	-	46(22)	68(15)
1km	All	32(59)	44(32)	25(27)	-	-
	Spring	-	-	-	21(26)	58(33)
	Summer	-	-	-	27(36)	47(23)
	Autumn	-	-	-	28(40)	50(19)
	Winter	-	-	-	24(30)	52(29)
600m	All	27(82)	35(42)	22(40)	-	-
	Spring	-	-	-	16(36)	58(46)
	Summer	-	-	-	22(53)	48(29)
	Autumn	-	-	-	23(59)	51(23)
	Winter	-	-	-	21(49)	49(33)
200m	All	15(76)	19(36)	13(40)	-	-
	Spring	-	-	-	9(32)	31(44)
	Summer	-	-	-	13(50)	26(26)
	Autumn	-	-	-	13(56)	30(20)
	Winter	-	-	-	13(50)	23(112)

Table VIII.VIa Percentages of 5km, stretches of riverbank in two vegetation types in the upper Tyne catchment between 1993 and 1995. Values are given for the overall sample, for the North and South Tyne separately and for stretches with no otter signs (Absent) and stretches with otter signs (Present) in four seasons. VEG1, non-wooded; VEG2, wooded.

Season	Vegetation class	Percentage of stretches % (n)				
		All stretches	South Tyne	North Tyne	Absent	Present
Spring	VEG1	45(18)	44(7)	46(11)	67(12)	27(6)
	VEG2	55(22)	56(9)	54(13)	33(6)	73(16)
Summer	VEG1	50(20)	50(8)	50(12)	72(18)	13(2)
	VEG2	50(20)	50(8)	50(12)	28(7)	87(13)
Autumn	VEG1	43(17)	38(6)	46(11)	65(15)	12(2)
	VEG2	42(21)	62(10)	54(13)	35(8)	88(15)
Winter	VEG1	42(21)	56(9)	50(12)	61(17)	33(4)
	VEG2	58(19)	44(7)	50(12)	39(11)	67(8)

Table VIII.VIb Percentages of 2.5km stretches of riverbank in five vegetation types in the upper Tyne catchment between 1993 and 1995. Values are given for the overall sample, for the North and South Tyne separately and for stretches with no otter signs (Absent) and stretches with otter signs (Present) in four seasons. VEG1, bare ground and vegetation <0.1m (bare only in winter); VEG2, vegetation >0.1m≤1m in height (vegetation <0.1m in winter); VEG3, vegetation >1m, shrubs and open canopy woodland (vegetation >0.1m≤1m in height in winter); VEG4, closed canopy woodland (vegetation >1m, shrubs and open canopy woodland in winter); VEG5 closed canopy woodland (winter only)

Season	Altitude class	Percentage of stretches % (n)				
		All stretches	South Tyne	North Tyne	Absent	Present
Spring	VEG1	23(16)	39(11)	12(5)	38(14)	6(2)
	VEG2	26(18)	4(1)	40(17)	35(13)	15(5)
	VEG3	34(24)	32(9)	36(15)	22(8)	48(16)
	VEG4	17(12)	25(7)	12(5)	5(2)	30(10)
Summer	VEG1	13(9)	21(6)	7(3)	18(8)	4(1)
	VEG2	34(24)	21(6)	43(18)	44(20)	16(4)
	VEG3	34(24)	29(8)	38(16)	31(14)	40(10)
	VEG4	19(13)	29(8)	12(5)	7(3)	40(10)
Autumn	VEG1	26(18)	36(10)	19(8)	33(17)	6(1)
	VEG2	24(17)	14(4)	31(13)	29(15)	11(2)
	VEG3	31(22)	29(8)	33(14)	29(15)	39(7)
	VEG4	19(13)	21(6)	17(7)	10(5)	44(8)
Winter	VEG1	20(14)	39(11)	7(3)	29(14)	0(0)
	VEG2	14(10)	4(1)	21(9)	15(7)	14(3)
	VEG3	16(11)	4(1)	24(10)	21(10)	5(1)
	VEG4	31(22)	25(7)	36(15)	23(11)	50(11)
	VEG5	19(13)	29(8)	14(6)	13(6)	32(7)

Table VIII.VIc Percentages of 1km stretches of riverbank in six vegetation types in the upper Tyne catchment between 1993 and 1995. Values are given for the overall sample, for the North and South Tyne separately and for stretches with no otter signs (Absent) and stretches with otter signs (Present) in four seasons. VEG1, bare ground VEG2, vegetation <0.1m in height; VEG3, vegetation >0.1m≤1m in height; VEG4, vegetation >1m in height and shrubs; VEG5, open canopy woodland; VEG6, closed canopy woodland.

Season	Altitude class	Percentage of stretches % (n)				
		All stretches	South Tyne	North Tyne	Absent	Present
Spring	VEG1	11(20)	18(13)	6(7)	11(14)	11(6)
	VEG2	11(20)	16(12)	7(8)	16(20)	0(0)
	VEG3	20(37)	3(2)	32(35)	26(32)	9(5)
	VEG4	7(13)	14(10)	3(3)	7(9)	7(4)
	VEG5	30(54)	23(17)	34(37)	24(30)	42(24)
	VEG6	21(38)	26(19)	17(19)	16(20)	32(18)
Summer	VEG1	6(11)	8(6)	5(5)	8(10)	2(1)
	VEG2	9(17)	15(11)	6(6)	12(16)	2(1)
	VEG3	25(45)	14(10)	32(35)	30(40)	10(5)
	VEG4	11(20)	16(12)	7(8)	9(12)	16(8)
	VEG5	28(51)	19(14)	34(37)	25(33)	37(18)
	VEG6	21(38)	27(20)	17(18)	17(22)	33(16)
Autumn	VEG1	10(18)	19(14)	4(4)	11(16)	5(2)
	VEG2	13(24)	15(11)	12(13)	15(22)	5(2)
	VEG3	21(38)	7(5)	30(33)	25(36)	5(2)
	VEG4	8(15)	15(11)	4(4)	8(11)	11(4)
	VEG5	27(50)	18(13)	34(37)	26(37)	34(13)
	VEG6	20(37)	26(19)	17(18)	15(22)	39(15)
Winter	VEG1	19(34)	30(22)	11(12)	24(30)	7(4)
	VEG2	12(21)	7(5)	15(16)	11(14)	5(3)
	VEG3	14(26)	5(4)	20(22)	18(23)	5(3)
	VEG4	6(11)	12(9)	2(2)	6(8)	5(3)
	VEG5	30(54)	21(15)	36(39)	25(32)	39(22)
	VEG6	20(36)	25(18)	17(18)	39(49)	38(21)

Table VIII.VId Percentages of 600m stretches of riverbank in six vegetation types in the upper Tyne catchment between 1993 and 1995. Values are given for the overall sample, for the North and South Tyne separately and for stretches with no otter signs (Absent) and stretches with otter signs (Present) in four seasons. VEG1, bare ground VEG2, vegetation <0.1m in height; VEG3, vegetation >0.1m≤1m in height; VEG4, vegetation >1m in height and shrubs; VEG5, open canopy woodland; VEG6, closed canopy woodland.

Season	Altitude class	Percentage of stretches % (n)				
		All stretches	South Tyne	North Tyne	Absent	Present
Spring	VEG1	20(60)	18(22)	21(38)	22(50)	13(10)
	VEG2	22(66)	16(19)	26(47)	26(58)	10(8)
	VEG3	6(19)	8(9)	5(10)	6(13)	8(6)
	VEG4	6(19)	11(13)	3(6)	7(15)	5(4)
	VEG5	28(86)	28(33)	29(53)	25(56)	38(30)
	VEG6	18(54)	20(24)	16(30)	14(32)	28(22)
Summer	VEG1	6(19)	8(10)	5(9)	7(18)	2(1)
	VEG2	46(39)	16(19)	11(20)	15(37)	3(2)
	VEG3	24(73)	18(22)	28(51)	27(67)	10(6)
	VEG4	10(31)	12(14)	9(17)	11(26)	8(5)
	VEG5	31(43)	27(32)	33(61)	26(64)	48(29)
	VEG6	16(49)	19(23)	14(26)	13(32)	28(17)
Autumn	VEG1	14(42)	22(26)	9(16)	15(40)	4(2)
	VEG2	10(30)	12(14)	9(16)	11(29)	2(1)
	VEG3	21(63)	10(12)	28(51)	22(58)	11(5)
	VEG4	9(26)	10(12)	8(14)	9(24)	4(2)
	VEG5	30(91)	26(31)	33(60)	27(70)	47(21)
	VEG6	17(52)	21(25)	15(27)	15(38)	31(14)
Winter	VEG1	22(66)	37(44)	12(22)	24(56)	15(10)
	VEG2	11(34)	6(7)	15(27)	13(31)	4(3)
	VEG3	17(51)	6(7)	24(44)	18(43)	12(8)
	VEG4	4(13)	8(9)	2(4)	4(10)	4(3)
	VEG5	30(92)	25(30)	34(62)	28(67)	37(25)
	VEG6	16(48)	19(23)	14(25)	12(29)	28(19)

Table VIII.VIe Percentages of 200m stretches of riverbank in five vegetation types in the upper Tyne catchment between 1993 and 1995. Values are given for the overall sample, for the North and South Tyne separately and for stretches with no otter signs (Absent) and stretches with otter signs (Present) in four seasons. VEG1, bare ground and vegetation <0.1m; VEG2, vegetation >0.1m≤1m in height; VEG3, vegetation >1m, shrubs and open canopy woodland; VEG4, closed canopy woodland.

Season	Altitude class	Percentage of stretches % (n)				
		All stretches	South Tyne	North Tyne	Absent	Present
Spring	VEG1	21(107)	31(61)	15(46)	26(92)	11(15)
	VEG2	18(91)	7(14)	25(77)	22(80)	8(11)
	VEG3	38(188)	37(17)	38(117)	34(123)	46(65)
	VEG4	22(112)	25(48)	21(64)	18(65)	35(49)
Summer	VEG1	17(84)	25(49)	12(35)	11(45)	6(6)
	VEG2	21(107)	15(29)	26(78)	8(33)	10(10)
	VEG3	40(200)	35(68)	43(132)	38(154)	46(46)
	VEG4	21(107)	25(48)	19(59)	17(69)	78(78)
Autumn	VEG1	19(85)	27(53)	14(42)	21(89)	9(6)
	VEG2	19(96)	7(15)	27(81)	21(90)	9(6)
	VEG3	37(186)	36(70)	38(116)	37(158)	42(28)
	VEG4	24(121)	29(56)	21(65)	22(95)	39(26)
Winter	VEG1	29(142)	33(64)	26(78)	31(120)	20(22)
	VEG2	11(56)	6(11)	15(45)	11(43)	12(13)
	VEG3	38(190)	36(70)	39(120)	37(144)	41(46)
	VEG4	22(110)	25(49)	20(61)	20(79)	28(31)

Table VIII.VIIa Percentages of 5km stretches of river containing a number of fish species in the upper Tyne catchment between 1993 and 1995. Values are given for the overall sample, for the North and South Tyne separately and for stretches with no otter signs (Abs) and stretches with otter signs (Pres) in the summer only.

Species	Fish density class	Percentage of stretches % (n)				
		All	South Tyne	North Tyne	Abs	Pres
Eel	Absent	12(4)	13(2)	11(2)	15(3)	8(1)
	Present	78(29)	87(13)	89(16)	85(17)	92(12)
Minnow	Absent	42(14)	73(11)	17(3)	55(11)	23(3)
	Present	58(19)	27(4)	83(15)	45(9)	77(10)
Salmon	Absent	48(16)	73(11)	28(5)	70(14)	15(2)
	Present	52(17)	27(4)	72(13)	30(6)	85(11)
Trout	Absent	39(13)	20(3)	56(10)	30(6)	54(7)
(>70≤90mm)	Present	61(20)	80(12)	44(8)	70(14)	46(6)
Salmonids	Absent	27(9)	20(3)	33(6)	25(5)	31(4)
(>70≤90mm)	Present	73(24)	80(12)	67(12)	75(15)	69(9)
	≤15 fish100m^{-2}	42(14)	27(4)	56(10)	40(8)	46(6)
Total trout	>15≤50 fish100m^{-2}	24(8)	33(5)	17(3)	20(4)	31(4)
	>50 fish100m^{-2}	34(11)	40(6)	28(5)	40(8)	23(3)
	≤15 fish100m^{-2}	30(10)	27(4)	33(6)	25(5)	38(5)
Total salmonid	>15≤50 fish100m^{-2}	33(11)	33(5)	33(6)	30(6)	38(5)
	>50 fish100m^{-2}	37(12)	40(6)	33(6)	45(9)	23(3)
	Absent	42(14)	53(8)	33(6)	45(9)	38(5)
Stoneloach	>5≤25 fish100m^{-2}	30(10)	27(4)	33(6)	35(7)	23(3)
	>25 fish100m^{-2}	28(9)	20(3)	33(6)	20(4)	38(5)

Table VIII.VIIb Percentages of 2.5km stretches of river containing a number of fish species in the upper Tyne catchment in the summer of 1995. Values are given for the overall sample, for the North and South Tyne separately and for stretches with no otter signs (Abs) and stretches with otter signs (Pres) in the summer of 1993.

Species	Fish density class	Percentage of stretches % (n)				
		All	South Tyne	North Tyne	Abs	Pres
Eel	Absent	24(14)	33(8)	17(6)	33(12)	9(2)
	Present	76(45)	67(16)	83(29)	67(24)	91(21)
Minnow	Absent	46(27)	75(18)	26(9)	56(20)	30(7)
	Present	54(32)	25(6)	74(26)	44(16)	70(16)
Salmon	Absent	64(38)	83(20)	51(18)	27(75)	48(11)
	Present	36(21)	17(4)	49(17)	25(9)	52(12)
Trout	Absent	61(36)	46(11)	71(25)	53(19)	74(17)
(>70≤90mm)	Present	39(23)	54(13)	29(10)	47(17)	26(6)
Salmonids	Absent	54(32)	42(10)	63(22)	50(18)	61(14)
(>70≤90mm)	Present	46(27)	58(14)	37(13)	50(18)	39(9)
Stoneloach	Absent	29(17)	33(8)	26(9)	44(16)	1(4)
	>5≤25 fish100m^{-2}	34(20)	25(6)	49(14)	28(10)	44(10)
	>25 fish100m^{-2}	37(22)	42(10)	34(12)	28(10)	52(12)

Table VIII.VIIc Mean fish density (No.100m^{-2}) of trout and total salmonids in 2.5km stretches in the upper Tyne catchment in the summer of 1995. Mean and standard error values are given for the overall sample, for the North and South Tyne separately and for stretches with no otter signs (Absent) and stretches with otter signs (Present) in the summer of 1993. These values were calculated after back transformation from log-transformed variables.

Species	Mean (SE)				
	All stretches	South Tyne	North Tyne	Absent	Present
Trout	11.6(0.3)	23.2(0.4)	7.1(0.4)	17.5(0.3)	5.9(0.4)
Salmonids	18.0(0.2)	26.3(0.3)	13.8(0.3)	22.4(0.3)	12.8(0.3)

Table VIII.VIId Percentages of 1km stretches of river containing a number of fish species in the upper Tyne catchment in the summer of 1995. Values are given for the overall sample, for the North and South Tyne separately and for stretches with no otter signs (Abs) and stretches with otter signs (Pres) in the summer of 1993.

Species	Fish density class	Percentage of stretches % (n)				
		All	South Tyne	North Tyne	Abs	Pres
Eel	Absent	35(29)	44(16)	28(13)	41(24)	20(5)
	Present	65(54)	56(20)	72(34)	59(34)	80(20)
Minnow	Absent	47(39)	81(29)	21(10)	64(37)	8(2)
	Present	53(44)	19(7)	79(37)	36(21)	92(23)
Salmon	Absent	70(58)	86(31)	57(27)	79(46)	48(12)
	Present	30(25)	14(5)	43(20)	21(12)	52(13)
Trout	Absent	64(53)	53(19)	72(34)	57(33)	80(20)
(>70≤90mm)	Present	36(30)	47(17)	28(13)	43(25)	20(5)
Salmonids	Absent	57(47)	50(18)	62(29)	52(30)	68(17)
(>70≤90mm)	Present	43(36)	50(18)	38(18)	48(28)	32(8)
	Absent	36(30)	42(15)	32(15)	47(27)	12(3)
Stoneloach	>5≤25 fish100m^{-2}	30(25)	19(7)	38(18)	26(15)	40(10)
	>25 fish100m^{-2}	34(28)	39(14)	30(14)	28(16)	48(12)

Table VIII.VIIe Mean fish density (No.100m^{-2}) of trout and total salmonids in 1km stretches in the upper Tyne catchment in the summer of 1995. Mean and standard error values are given for the overall sample, for the North and South Tyne separately and for stretches with no otter signs (Absent) and stretches with otter signs (Present) in the summer of 1993. These values were calculated after back transformation from log-transformed variables.

Species	Mean (SE)				
	All stretches	South Tyne	North Tyne	Absent	Present
Trout	11.4(0.2)	24.7(0.3)	6.1(0.3)	15.7(0.3)	5.3(0.4)
Salmonids	17.1(0.2)	28.5(0.3)	11.4(0.3)	20.4(0.3)	11.2(0.4)

Table VIII.VIIf Percentages of 600m stretches of river containing a number of fish species in the upper Tyne catchment in the summer of 1995. Values are given for the overall sample, for the North and South Tyne separately and for stretches with no otter signs (Abs) and stretches with otter signs (Pres) in the summer of 1993.

Species	Fish density class	Percentage of stretches % (n)				
		All	South Tyne	North Tyne	Abs	Pres
Eel	Absent	35(28)	46(16)	27(12)	41(24)	19(4)
	Present	65(51)	54(19)	73(32)	59(34)	81(17)
Minnow	Absent	47(37)	80(28)	20(9)	62(36)	5(1)
	Present	53(42)	20(7)	80(35)	38(22)	95(20)
Salmon	Absent	70(55)	89(31)	55(24)	76(44)	52(11)
	Present	30(24)	11(4)	46(20)	24(14)	48(10)
Trout	Absent	62(49)	51(18)	71(31)	57(33)	76(16)
(>70≤90mm)	Present	38(30)	49(17)	30(13)	43(25)	24(5)
Salmonids	Absent	57(45)	49(17)	64(28)	52(30)	71(15)
(>70≤90mm)	Present	43(34)	51(18)	36(16)	48(28)	29(6)
Stoneloach	Absent	37(29)	46(16)	30(13)	47(27)	10(2)
	>5≤25 fish100m^{-2}	34(27)	26(9)	41(18)	24(14)	62(13)
	>25 fish100m^{-2}	29(23)	29(10)	30(13)	29(17)	29(6)

Table VIII.VIIg Mean fish density (No.100m^{-2}) of trout and total salmonids in 600m stretches in the upper Tyne catchment in the summer of 1995. Mean and standard error values are given for the overall sample, for the North and South Tyne separately and for stretches with no otter signs (Absent) and stretches with otter signs (Present) in the summer of 1993. These values were calculated after back transformation from log-transformed variables.

Species	Mean (SE)				
	All stretches	South Tyne	North Tyne	Absent	Present
Trout	10.9(0.2)	24.0(0.3)	5.6(0.3)	13.6(0.3)	5.8(0.5)
Salmonids	16.4(0.2)	27.9(0.3)	10.6(0.3)	19.6(0.2)	9.9(0.4)

Table VIII.VIIh Percentages of 200m stretches of river containing a number of fish species in the upper Tyne catchment in the summer of 1995. Values are given for the overall sample, for the North and South Tyne separately and for stretches with no otter signs (Abs) and stretches with otter signs (Pres) in the summer of 1993.

Species	Fish density class	Percentage of stretches % (n)				
		All	South Tyne	North Tyne	Abs	Pres
Eel	Absent	32(23)	48(15)	20(8)	37(21)	13(2)
	Present	68(49)	52(16)	80(33)	63(36)	87(13)
Minnow	Absent	46(33)	81(25)	20(80	54(31)	13(2)
	Present	54(39)	19(6)	80(33)	46(26)	87(13)
Salmon	Absent	68(49)	84(26)	56(23)	68(39)	67(10)
	Present	32(23)	16(5)	44(18)	32(18)	33(5)
Trout	Absent	69(50)	55(17)	80(33)	68(39)	73(11)
(>70≤90mm)	Present	31(22)	45(14)	20(8)	32(18)	27(4)
Salmonids	Absent	64(46)	55(17)	71(29)	63(36)	67(10)
(>70≤90mm)	Present	36(26)	45(14)	29(12)	37(21)	33(5)
	Absent	36(26)	45(14)	29(12)	42(24)	13(2)
Stoneloach	>5≤25 fish100m^{-2}	36(26)	29(9)	42(17)	20(35)	60(9)
	>25 fish100m^{-2}	28(20)	26(8)	29(12)	26(15)	33(5)

Table VIII.VIIi Mean fish density (No.100m^{-2}) of trout and total salmonids in 200m stretches in the upper Tyne catchment in the summer of 1995. Mean and standard error values are given for the overall sample, for the North and South Tyne separately and for stretches with no otter signs (Absent) and stretches with otter signs (Present) in the summer of 1993. These values were calculated after back transformation from log-transformed variables.

Species	Mean (SE)				
	All stretches	South Tyne	North Tyne	Absent	Present
Trout	10.0(0.2)	22.0(0.4)	5.3(0.3)	10.0(0.3)	10.1(0.6)
Salmonids	15.1(0.2)	25.9(0.3)	9.9(0.3)	16.1(0.3)	11.8(0.6)

Table VIII.VIIIa Mean heavy metal concentrations (in μg/g of tissue) in liver and muscle tissue of eels caught during an electro-fishing survey of the upper Tyne catchment in the summer of 1995. Mean and standard error values are given for the overall sample and for the North and South Tyne. These values were calculated after back transformation from log-transformed variables.

Tissue	Metal	Mean (SE)		
		All stretches	South Tyne	North Tyne
Muscle	Cadmium	1.01(1.0)	1.19(1.1)	0.91(1.1)
	Copper	1.39(1.1)	1.75(1.1)	1.19(1.1)
	Lead	2.20(1.0)	2.50(1.1)	2.01(1.0)
	Zinc	85.1(1.1)	107.4(1.1)	72.9(1.1)
Liver	Cadmium	7.24(1.1)	8.57(1.2)	6.46(1.1)
	Copper	119.4(1.1)	138.0(1.1)	108.4(1.1)
	Lead	9.89(1.1)	17.3(1.2)	6.81(1.1)
	Zinc	302.0(1.0)	343.6(1.1)	277.3(1.1)

Table VIII.VIIIb Mean heavy metal concentrations (in μg/g of tissue) in liver and muscle tissue of eels caught during an electro-fishing survey of the upper Tyne catchment in the summer of 1995. Mean and standard error values are given for the concentrations of metals in stretches of riverbank with or without otter signs in 5km sample units in four surveys between 1993 and 1994. These values were calculated after back transformation from log-transformed variables.

Season	Metal	Mean (SE)			
		Absent		Present	
		Muscle	Liver	Muscle	Liver
Spring	Cadmium	1.03(1.1)	5.93(1.2)	1.04(1.1)	9.71(1.1)
	Copper	1.29(1.1)	115.9(1.1)	1.35(1.1)	114.0(1.2)
	Lead	2.11(1.1)	11.0(1.3)	2.21(1.1)	10.2(1.2)
	Zinc	79.8(1.1)	307.6(1.1)	78.9(1.2)	312.6(1.1)
Summer	Cadmium	1.06(1.1)	7.01(1.2)	1.01(1.1)	9.3(1.1)
	Copper	1.3(1.1)	121.9(1.1)	1.32(1.1)	105.6(1.3)
	Lead	2.17(1.1)	12.4(1.2)	2.17(1.1)	8.45(1.1)
	Zinc	84.9(1.1)	319.2(1.1)	72.1(1.3)	299.2(1.1)
Autumn	Cadmium	0.97(1.1)	7.05(1.2)	1.11(1.1)	8.81(1.1)
	Copper	1.18(1.1)	124.2(1.1)	1.30(1.1)	106.2(1.2)
	Lead	2.11(1.1)	11.7(1.3)	2.22(1.0)	9.44(1.2)
	Zinc	77.3(1.1)	318.4(1.1)	85.1(1.1)	302.7(1.1)
Winter	Cadmium	1.07(1.1)	7.94(1.2)	0.98(1.1)	7.74(1.1)
	Copper	1.30(1.1)	130.9(1.1)	1.39(1.1)	85.5(1.4)
	Lead	2.22(1.1)	12.8(1.2)	2.06(1.1)	6.81(1.1)
	Zinc	85.1(1.1)	325.8(1.1)	67.5(1.4)	277.9(1.1)

Table VIII.VIIIc Mean heavy metal concentrations (in μg/g of tissue) in liver and muscle tissue of eels caught during an electro-fishing survey of the upper Tyne catchment in the summer of 1995. Mean and standard error values are given for the concentrations of metals in stretches of riverbank with or without otter signs in 2.5km sample units in four surveys between 1993 and 1994. These values were calculated after back transformation from log-transformed variables.

Season	Metal	Mean (SE)			
		Absent		Present	
		Muscle	Liver	Muscle	Liver
Spring	Cadmium	1.07(1.1)	7.50(1.2)	1.02(1.1)	7.52(1.2)
	Copper	1.30(1.1)	115.6(1.1)	1.39(1.1)	113.0(1.1)
	Lead	2.26(1.1)	10.8(1.2)	2.2(1.1)	9.93(1.2)
	Zinc	75.3(1.2)	296.5(1.1)	87.5(1.1)	286.4(1.1)
Summer	Cadmium	1.10(1.1)	5.7(1.2)	1.0(1.1)	10.1(1.1)
	Copper	1.26(1.1)	105.7(1.2)	1.46(1.0)	124.2(1.1)
	Lead	2.29(1.1)	9.7(1.2)	2.13(1.1)	11.1(1.2)
	Zinc	84.3(1.1)	276.1(1.1)	79.1(1.2)	306.9(1.1)
Autumn	Cadmium	1.11(1.1)	7.05(1.2)	0.90(1.0)	8.83(1.1)
	Copper	1.37(1.0)	116.1(1.1)	1.29(1.1)	109.4(1.1)
	Lead	2.30(1.1)	10.9(1.2)	2.00(1.1)	9.12(1.2)
	Zinc	87.1(1.1)	295.8(1.1)	69.5(1.3)	279.9(1.1)
Winter	Cadmium	1.08(1.1)	7.33(1.2)	0.99(1.1)	7.78(1.2)
	Copper	1.34(1.1)	113.8(1.1)	1.37(1.1)	114.6(1.1)
	Lead	2.32(1.1)	10.7(1.2)	2.08(1.1)	9.89(1.2)
	Zinc	86.9(1.1)	287.7(1.1)	75.2(1.2)	295.1(1.1)

Table VIII.VIIId Mean heavy metal concentrations (in μg/g of tissue) in liver and muscle tissue of eels caught during an electro-fishing survey of the upper Tyne catchment in the summer of 1995. Mean and standard error values are given for the concentrations of metals in stretches of riverbank with or without otter signs in 1km sample units in four surveys between 1993 and 1994. These values were calculated after back transformation from log-transformed variables.

Season	Metal	Mean (SE)			
		Absent		Present	
		Muscle	Liver	Muscle	Liver
Spring	Cadmium	0.97(1.1)	6.79(1.1)	1.18(1.1)	4.99(1.4)
	Copper	1.32(1.1)	92.7(1.2)	1.50(1.1)	78.2(1.5)
	Lead	2.15(1.0)	9.04(1.1)	2.20(1.1)	8.43(1.3)
	Zinc	77.1(1.1)	290.4(1.1)	97.9(1.1)	244.9(1.2)
Summer	Cadmium	1.09(1.1)	6.31(1.2)	0.94(1.1)	5.90(1.3)
	Copper	1.42(1.1)	90.2(1.3)	1.28(1.1)	83.9(1.4)
	Lead	2.30(1.0)	10.4(1.2)	1.96(1.1)	6.37(1.1)
	Zinc	88.5(1.1)	292.4(1.1)	72.9(1.2)	243.8(1.2)
Autumn	Cadmium	1.09(1.1)	6.50(1.2)	0.87(1.1)	5.24(1.3)
	Copper	1.41(1.1)	89.9(1.2)	1.27(1.1)	82.0(1.6)
	Lead	2.31(1.0)	9.75(1.2)	1.85(1.1)	6.53(1.2)
	Zinc	82.2(1.1)	284.4(1.1)	85.3(1.1)	249.5(1.2)
Winter	Cadmium	1.04(1.1)	6.98(1.2)	1.00(1.1)	5.13(1.3)
	Copper	1.39(1.1)	95.5(1.3)	1.35(1.1)	77.6(1.4)
	Lead	2.21(1.1)	9.46(1.2)	2.14(1.1)	8.00(1.2)
	Zinc	84.9(1.1)	288.4(1.1)	80.2(1.2)	257.0(1.1)

Table VIII.IXa Percentages of 5km stretches of riverbank in the upper Tyne catchment containing several measures of human disturbance within a 100m buffer. Values are given for the overall sample and for the North and South Tyne separately. AROAD, presence of A-roads; BROAD1, total length of B-road ≥0<50m; BROAD2, total lenght of B-road ≥50<250m; BROAD3, total length of B-road > 250m; PATH1, total length of footpath and bridleway ≥0<50m; PATH2, total length of footpath and bridleway ≥50<200m; PATH3 total length of footpath and bridleway >200m; BUILD1 total area of buildings ≥0<500m^2; BUILD2 total area of buildings ≥500<1500m^2; BUILD3 total area of buildings ≥1500m^2.

	Percentage of stretches % (n)		
Variable	All	South Tyne	North Tyne
AROAD	42(17)	50(8)	37(9)
BROAD1	40(16)	25(4)	50(12)
BROAD2	38(15)	31(5)	42(10)
BROAD3	23(9)	44(7)	8(2)
PATH1	28(11)	19(3)	33(8)
PATH2	34(14)	50(8)	25(6)
PATH3	38(15)	31(5)	42(10)
BUILD1	33(13)	25(4)	38(9)
BUILD2	33(13)	44(7)	28(6)
BUILD3	34(14)	31(5)	38(9)

Table VIII.IXb Percentages of 5km stretches of riverbank in the upper Tyne catchment containing several measures of human disturbance within a 100m buffer. Values are given for stretches with (Present) and without (Absent) otter signs in four surveys between 1993 and 1994. AROAD, presence of A-roads; BROAD1, total length of B-road ≥0<50m; BROAD2, total lenght of B-road ≥50<250m; BROAD3, total length of B-road > 250m; PATH1, total length of footpath and bridleway ≥0<50m; PATH2, total length of footpath and bridleway ≥50<200m; PATH3 total length of footpath and bridleway >200m; BUILD1 total area of buildings ≥0<500m^2; BUILD2 total area of buildings ≥500<1500m^2; BUILD3 total area of buildings ≥1500m^2.

		Percentage of stretches % (n)					
Season	Variable	Absent	Present	Season	Variable	Absent	Present
Spring	AROAD	44(8)	41(9)	Autumn	AROAD	35(8)	53(9)
	BROAD1	50(9)	32(7)		BROAD1	48(11)	29(5)
	BROAD2	28(5)	46(10)		BROAD2	35(8)	41(7)
	BROAD3	22(4)	23(5)		BROAD3	17(4)	29(5)
	PATH1	39(7)	18(4)		PATH1	35(8)	18(3)
	PATH2	39(7)	32(7)		PATH2	30(7)	41(7)
	PATH3	22(4)	50(11)		PATH3	35(8)	41(7)
	BUILD1	50(9)	18(4)		BUILD1	44(10)	18(3)
	BUILD2	22(4)	41(9)		BUILD2	22(5)	47(8)
	BUILD3	28(5)	41(9)		BUILD3	35(8)	35(6)
Summer	AROAD	44(11)	40(6)	Winter	AROAD	43(12)	42(5)
	BROAD1	48(12)	27(4)		BROAD1	46(13)	25(3)
	BROAD2	28(7)	53(8)		BROAD2	32(9)	50(6)
	BROAD3	24(6)	20(3)		BROAD3	21(6)	25(3)
	PATH1	32(8)	20(3)		PATH1	32(9)	17(2)
	PATH2	32(8)	40(6)		PATH2	36(10)	33(4)
	PATH3	36(9)	40(6)		PATH3	32(9)	50(6)
	BUILD1	56(14)	13(2)		BUILD1	39(11)	17(2)
	BUILD2	28(7)	40(6)		BUILD2	25(7)	50(6)
	BUILD3	28(7)	47(7)		BUILD3	36(10)	33(4)

Table VIII.IXc Percentages of 2.5km stretches of riverbank in the upper Tyne catchment containing several measures of human disturbance within a 100m buffer. Values are given for the overall sample and for the North and South Tyne separately. AROAD, presence of A-roads; BROAD, presence or absence of B-roads; PATH1, total length of footpath and bridleway ≥0≤50m; PATH2, total length of footpath and bridleway >50≤150m; PATH3 total length of footpath and bridleway >150≤500m; PATH4 total length of footpath and bridleway >500m; BUILD1 no buildings; BUILD2 total area of buildings >0≤1000m^2; BUILD3 total area of buildings >1000≤3000m^2; BUILD4 total area of buildings >3000m^2.

Variable	Percentage of stretches % (n)		
	All	South Tyne	North Tyne
AROAD	30(21)	25(7)	33(14)
BROAD	56(39)	79(22)	40(17)
PATH1	26(18)	21(6)	29(12)
PATH2	30(21)	39(11)	24(10)
PATH3	27(19)	25(7)	29(12)
PATH4	17(12)	14(4)	19(8)
BUILD1	27(19)	11(3)	38(16)
BUILD2	23(16)	25(7)	21(9)
BUILD3	29(20)	46(13)	17(7)
BUILD4	21(15)	18(5)	24(10)

Table VIII.IXd Percentages of 2.5km stretches of riverbank in the upper Tyne catchment containing several measures of human disturbance within a 100m buffer. Values are given for stretches with (Present) and without (Absent) otter signs in four surveys between 1993 and 1994. AROAD, presence of A-roads; BROAD, presence or absence of B-roads; PATH1, total length of footpath and bridleway ≥0≤50m; PATH2, total length of footpath and bridleway >50≤150m; PATH3 total length of footpath and bridleway >150≤500m; PATH4 total length of footpath and bridleway >500m; BUILD1 no buildings; BUILD2 total area of buildings >0≤1000m^2; BUILD3 total area of buildings >1000≤3000m^2; BUILD4 total area of buildings >3000m^2.

		Percentage of stretches % (n)					
Season	Variable	Absent	Present	Season	Variable	Absent	Present
Spring	AROAD	38(14)	21(7)	Autumn	AROAD	31(16)	28(5)
	BROAD	54(20)	58(19)		BROAD	52(27)	67(12)
	PATH1	38(14)	12(4)		PATH1	31(16)	11(2)
	PATH2	19(7)	42(14)		PATH2	27(14)	39(7)
	PATH3	27(10)	27(9)		PATH3	25(13)	33(6)
	PATH4	16(6)	18(6)		PATH4	17(9)	17(3)
	BUILD1	32(12)	21(7)		BUILD1	29(15)	22(4)
	BUILD2	22(8)	24(8)		BUILD2	23(12)	22(4)
	BUILD3	27(10)	30(10)		BUILD3	31(16)	22(4)
	BUILD4	19(7)	24(8)		BUILD4	17(4)	33(6)
Summer	AROAD	29(13)	32(8)	Winter	AROAD	31(15)	27(6)
	BROAD	51(23)	64(16)		BROAD	52(25)	64(14)
	PATH1	33(15)	12(3)		PATH1	29(14)	18(4)
	PATH2	27(12)	36(9)		PATH2	27(13)	36(8)
	PATH3	24(11)	32(8)		PATH3	25(12)	32(7)
	PATH4	16(7)	20(5)		PATH4	19(9)	14(3)
	BUILD1	33(15)	16(4)		BUILD1	31(15)	18(4)
	BUILD2	29(13)	12(3)		BUILD2	25(12)	18(4)
	BUILD3	27(12)	32(8)		BUILD3	25(12)	36(8)
	BUILD4	11(5)	40(10		BUILD4	19(9)	27(6)

Table VIII.IXe Percentages of 1km stretches of riverbank in the upper Tyne catchment containing several measures of human disturbance within a 100m buffer. Values are given for the overall sample and for the North and South Tyne separately. AROAD, presence of A-roads; BROAD, presence or absence of B-roads; PATH1, total length of footpath and bridleway ≥0≤50m; PATH2, total length of footpath and bridleway >50≤150m; PATH3 total length of footpath and bridleway >150≤500m; PATH4 total length of footpath and bridleway >500m; BUILD1 no buildings; BUILD2 total area of buildings >0≤1000m^2; BUILD3 total area of buildings >1000≤3000m^2; BUILD4 total area of buildings >3000m^2.

	Percentage of stretches % (n)		
Variable	All	South Tyne	North Tyne
AROAD	17(30)	15(11)	17(19)
BROAD	34(61)	52(38)	21(23)
PATH1	30(54)	16(12)	39(42)
PATH2	32(59)	41(30)	27(29)
PATH3	24(44)	27(20)	22(24)
PATH4	14(25)	15(11)	13(14)
BUILD1	55(100)	38(28)	66(72)
BUILD2	18(33)	23(17)	15(16)
BUILD3	18(32)	27(20)	11(12)
BUILD4	9(17)	11(8)	8(9)

Table VIII.IXf Percentages of 1km stretches of riverbank in the upper Tyne catchment containing several measures of human disturbance within a 100m buffer. Values are given for stretches with (Present) and without (Absent) otter signs in four surveys between 1993 and 1994. AROAD, presence of A-roads; BROAD, presence or absence of B-roads; PATH1, total length of footpath and bridleway ≥0≤50m; PATH2, total length of footpath and bridleway >50≤150m; PATH3 total length of footpath and bridleway >150≤500m; PATH4 total length of footpath and bridleway >500m; BUILD1 no buildings; BUILD2 total area of buildings >0≤1000m^2; BUILD3 total area of buildings >1000≤3000m^2; BUILD4 total area of buildings >3000m^2.

		Percentage of stretches % (n)					
Season	Variable	Absent	Present	Season	Variable	Absent	Present
Spring	AROAD	16(20)	18(10)	Autumn	AROAD	17(25)	13(5)
	BROAD	33(41)	35(20)		BROAD	33(48)	34(13)
	PATH1	28(35)	33(19)		PATH1	27(39)	40(15)
	PATH2	38(47)	21(12)		PATH2	33(48)	29(11)
	PATH3	22(27)	30(17)		PATH3	26(38)	16(6)
	PATH4	13(16)	16(9)		PATH4	13(19)	16(6)
	BUILD1	56(70)	53(30)		BUILD1	54(78)	58(22)
	BUILD2	18(23)	18(10)		BUILD2	19(28)	13(5)
	BUILD3	17(21)	19(11)		BUILD3	17(24)	21(8)
	BUILD4	9(11)	11(6)		BUILD4	10(14)	8(3)
Summer	AROAD	17(22)	16(8)	Winter	AROAD	16(20)	18(10)
	BROAD	34(45)	33(16)		BROAD	35(44)	30(17)
	PATH1	28(37)	35(17)		PATH1	25(32)	39(22)
	PATH2	35(43)	25(12)		PATH2	33(41)	32(18)
	PATH3	25(33)	22(11)		PATH3	30(37)	13(7)
	PATH4	12(16)	18(9)		PATH4	13(16)	16(9)
	BUILD1	54(72)	57(28)		BUILD1	58(73)	48(27)
	BUILD2	19(25)	16(8)		BUILD2	18(23)	18(10)
	BUILD3	17(22)	20(10)		BUILD3	16(20)	21(12)
	BUILD4	11(14)	6(3)		BUILD4	8(10)	13(7)

Table VIII.IXg Percentages of 600m stretches of riverbank in the upper Tyne catchment containing several measures of human disturbance within a 100m buffer. Values are given for the overall sample and for the North and South Tyne separately. AROAD, presence of A-roads; BROAD, presence or absence of B-roads; AROAD, presence of A-roads; BROAD, presence or absence of B-roads; PATH, presence of paths or bridleways; BUILD, presence or absence of buildings.

	Percentage of stretches % (n)		
Variable	All	South Tyne	North Tyne
AROAD	2(7)	1(1)	3(6)
BROAD	14(42)	26(31)	6(11)
PATH	40(122)	54(65)	31(57)
BUILD	14(43)	23(28)	8(15)

Table VIII.IXh Percentages of 200m stretches of riverbank in the upper Tyne catchment containing several measures of human disturbance within a 100m buffer. Values are given for stretches with (Present) and without (Absent) otter signs in four surveys between 1993 and 1994. AROAD, presence of A-roads; BROAD, presence or absence of B-roads; PATH, presence of paths or bridleways; BUILD, presence or absence of buildings.

		Percentage of stretches % (n)	
Season	Variable	Absent	Present
Spring	AROAD	3(7)	0(0)
	BROAD	13(29)	16(13)
	PATH	43(97)	31(25)
	BUILD	15(33)	13(10)
Summer	AROAD	2(5)	3(2)
	BROAD	14(35)	12(7)
	PATH	43(104)	30(18)
	BUILD	15(36)	12(7)
Autumn	AROAD	2(6)	2(1)
	BROAD	14(35)	16(7)
	PATH	43(110)	27(12)
	BUILD	15(39)	9(4)
Winter	AROAD	2(5)	3(2)
	BROAD	13(31)	16(11)
	PATH	45(105)	25(17)
	BUILD	14(32)	16(11)

Table VIII.IXi Percentages of 200m stretches of riverbank in the upper Tyne catchment containing several measures of human disturbance within a 100m buffer. Values are given for the overall sample and for the North and South Tyne separately. AROAD, presence of A-roads; BROAD, presence or absence of B-roads; AROAD, presence of A-roads; BROAD, presence or absence of B-roads; PATH, presence of paths or bridleways; BUILD, presence or absence of buildings.

	Percentage of stretches % (n)		
Variable	All	South Tyne	North Tyne
AROAD	2(8)	<1(1)	2(7)
BROAD	7(35)	12(23)	4(12)
PATH	24(122)	29(57)	21(65)
BUILD	7(35)	12(24)	4(11)

Table VIII.IXj Percentages of 600m stretches of riverbank in the upper Tyne catchment containing several measures of human disturbance within a 100m buffer. Values are given for stretches with (Present) and without (Absent) otter signs in four surveys between 1993 and 1994. AROAD, presence of A-roads; BROAD, presence or absence of B-roads; PATH, presence of paths or bridleways; BUILD, presence or absence of buildings.

		Percentage of stretches % (n)	
Season	Variable	Absent	Present
Spring	AROAD	2(7)	<1(1)
	BROAD	7(25)	7(10)
	PATH	26(93)	21(29)
	BUILD	7(25)	7(10)
Summer	AROAD	1(5)	3(3)
	BROAD	7(29)	6(6)
	PATH	27(107)	15(15)
	BUILD	8(33)	2(2)
Autumn	AROAD	2(7)	2(1)
	BROAD	7(32)	5(3)
	PATH	27(115)	11(7)
	BUILD	8(33)	3(2)
Winter	AROAD	2(7)	<1(1)
	BROAD	8(28)	6(7)
	PATH	28(106)	7(8)
	BUILD	7(27)	14(16)